CRETACEOUS FAUNAS FROM ZULULAND AND NATAL, SOUTH AFRICA
THE AMMONITE SUBFAMILY BARROISICERATINAE BASSE, 1947

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(With 51 figures)

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ABSTRACT

Representatives of the subfamily Barroisiceratinae are locally common in the Coniacian of Zululand. The following are described: *Reesideoceras lornae* (van Hoepen, 1968), *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907), to which all previously named South African *F. (Forresteria)* and many other species are referred, *F. (F.) madagascariensis* (Collignon, 1965), *F. (F.)* cf. *hobsoni* (Reeside, 1932), *Yabeiceras orientale* Tokunaga & Shimizu, 1926, *Y.* cf. *orientale*, *Y. transiens* sp. nov., *Y. ankinatsyense* Collignon, 1965, *Y. costatum* Collignon, 1965, *Y. manasoaense* Collignon, 1965, *Y.* aff. *manasoaense*, *Y. crassiornatum* sp. nov., *Y. cobbani* sp. nov. and *Yabeiceras* sp. indet.

Itwebeoceras van Hoepen, 1968, is shown to be a synonym of *Reesidites* Wright & Matsumoto, 1954; *Zumpangoceras* Basse, 1947, *Collignonella* van Hoepen, 1957, *Basseoceras* van Hoepen, 1968, *Eedenoceras* van Hoepen, 1968, and *Neokanabiceras* Collignon, 1965, are synonyms of *Forresteria (Forresteria)*, and it is suggested that *Harleites* Reeside, 1932, is a senior synonym of *Reesideoceras* Basse, 1947.

CONTENTS

INTRODUCTION

The Barroisiceratinae are a small subfamily of the Collignoniceratidae derived from late Collignoniceratinae, perhaps via *Subprionocyclus* Shimizu. They vary from compressed and involute to evolute and inflated, and either

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have strong to weak ribs arising singly or in groups from bullae, or not. Ventrolateral and siphonal clavi are generally developed at some stage during ontogeny, the latter sometimes fusing into a keel. A lateral tubercle develops in some taxa and several lose virtually all ornament on the body whorl, which may be either tabular or compressed with fastigiate or tabulate venter. The sutures are generally simple with short, moderately incised saddles.

Within several genera large and small species with modified body chambers occur and are in some cases afforded subgeneric status. This may represent an as yet poorly perceived dimorphism: the evidence is still inconclusive.

The group as a whole differs from the ancestral Collignoniceratinae in having only one rather than two rows of ventrolateral nodes. On this basis *Reesidites* Wright & Matsumoto, 1954, belongs to this subfamily, which thus ranges from Upper Turonian through the Coniacian. The subfamily has a wide geographic distribution, and most members are taken as stratigraphic indicators of the Coniacian. As is clear from recent discussions by Hancock & Kennedy (1981) and Matsumoto (in Matsumoto *et al.* 1981: 63) amongst others, the true stratigraphic distribution of species and genera is still unsettled. The present firmly dated records from Zululand are thus of more than local significance. Added to this, the local abundance of one genus, *Forresteria* Reeside, 1932, allows a discussion of ontogenetic development and intraspecific variation that clarifies several taxonomic problems.

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the repositories of the material studied:

BMNH	British Museum (Natural History)
SAM	South African Museum, Cape Town
SAS	South African Geological Survey, Pretoria
USNM	National Museum of Natural History, Washington, D.C.

FIELD LOCALITIES

Details of localities mentioned in the text are given by Kennedy & Klinger (1975); fuller descriptions of sections are deposited in the Palaeontology Department of the British Museum (Natural History), London; Geological Survey, Pretoria; and the South African Museum, Cape Town.

DIMENSIONS OF SPECIMENS

All dimensions are given in millimetres:

D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter; *c* and *ic* refer to costal and intercostal measurements respectively.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916), reviewed by Kullman & Wiedmann (1970) is followed here:

I = internal lobe, U = umbilical lobe, L = lateral lobe, E = external lobe.

SYSTEMATIC PALAEONTOLOGY

Superfamily ACANTHOCERATACEAE de Grossouvre, 1894
Family **Collignoniceratidae** Wright & Wright, 1951
Subfamily Barroisiceratinae Basse, 1947

Genus *Reesidites* Wright & Matsumoto, 1954
(= *Itwebeoceras* van Hoepen, 1968)

Type species

Barroisiceras minimum Hayasaka & Fukada (1951: 325 (ex Yabe 1925, *nom. nud*)), from the Upper Turonian of Japan, by the original designation of Wright & Matsumoto (1954: 130).

Diagnosis

Involute, compressed, flat-sided sinuous ribs arise in groups of two or three from variably developed umbilical bullae. Shorter intercalated ribs are inserted on the middle to outer flank and all ribs bear strong ventrolateral clavi from which they project forward to prominent siphonal clavi. Ribs broaden and flatten with increasing age.

Suture with markedly asymmetric E/L in the type species at least.

Discussion

Reesidites has been discussed at length by Wright & Matsumoto (1954: 130), Obata (1965), and Matsumoto (1965: 61). There seems little doubt that *Reesidites minimus* and *R. elegans* Matsumoto & Inoma (1971: 139, pl. 23 (figs 1–3), text-figs 5–7) are derived from an involute collignoniceratid, probably *Subprionocyclus* (see e.g. Reyment 1975). The ornament of the two genera differs only in the presence of both inner *and* outer ventrolateral tubercles in the latter. The suture of *Subprionocyclus* (e.g. Matsumoto 1965, text-figs 28–30) already shows the asymmetry of E/L, that is so distinctively developed in *Reesidites*.

The ornament of *Reesidites minimus* differs little from that of *Barroisiceras haberfellneri* (von Hauer) (compare Fig. 1A and Fig. 1B–D), being a little more flexuous in *Reesidites* and projected strongly forward on the ventrolateral shoulder rather than straight. The sutures differ more obviously; in *B. haberfellneri* there is no comparable asymmetry (see Fig. 2). However, the type specimen of *Itwebeoceras lornae* van Hoepen, 1968, described below, has the ornament of *Reesidites* without sutural asymmetry. Taken together these obser-

Fig. 1. A. *Barroisiceras haberfellneri* (von Hauer, 1866). Geological Survey of Austria Collections 3764, from the Gosau Beds of Gams near Hieflau Austria. (Original of Von Hauer 1866: 30, pl. 1 (figs 1–2).) ×1. B–D. *Reesidites minimus* (Hayasaka & Fukada, 1951). B. University of Kyushu Collections H4089G bis, from the Upper Turonian of the Ikushumbets, Hokkaido. ×1. C–D. Holotype, Hokkaido University Collections, from the Upper Turonian of the Ikushumbets. ×1.

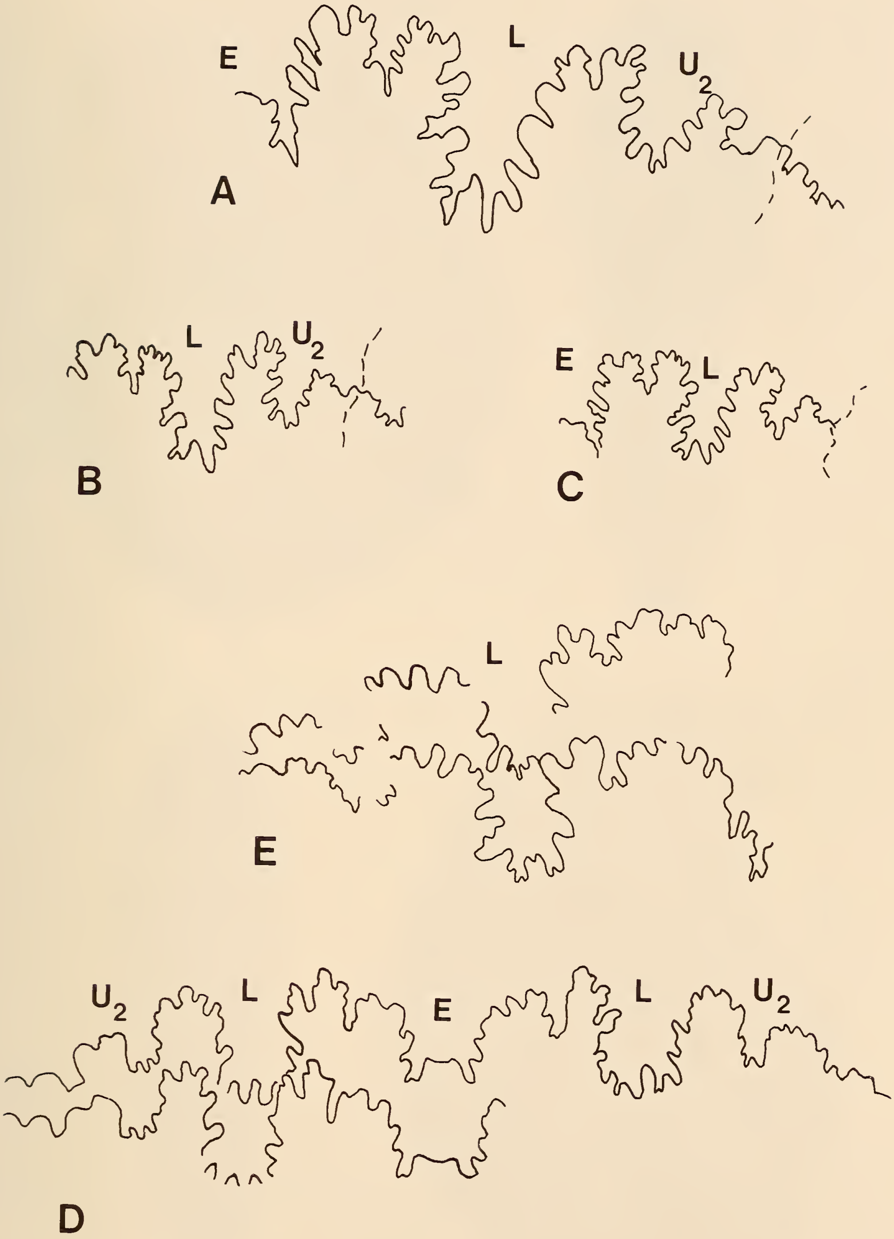

Fig. 2. A–C. *Reesidites lornae* (van Hoepen, 1968). Sutures of the holotype SAS Z1128. D. *Barroisiceras haberfellneri paeon* (Redtenbacher, 1873). Sutures of a specimen in the Geological Survey of Austria Collections 3481, from Ofenwald near Ströbl-Weissenbach, Austria. (Original of Redtenbacher 1873: 103, pl. 23 (fig. 3c–e).) E. *Reesidites minimus* (Hayasaka & Fukada, 1951). Sutures of the holotype. (After Matsumoto 1965: 65, text-fig. 36.) All ×2.

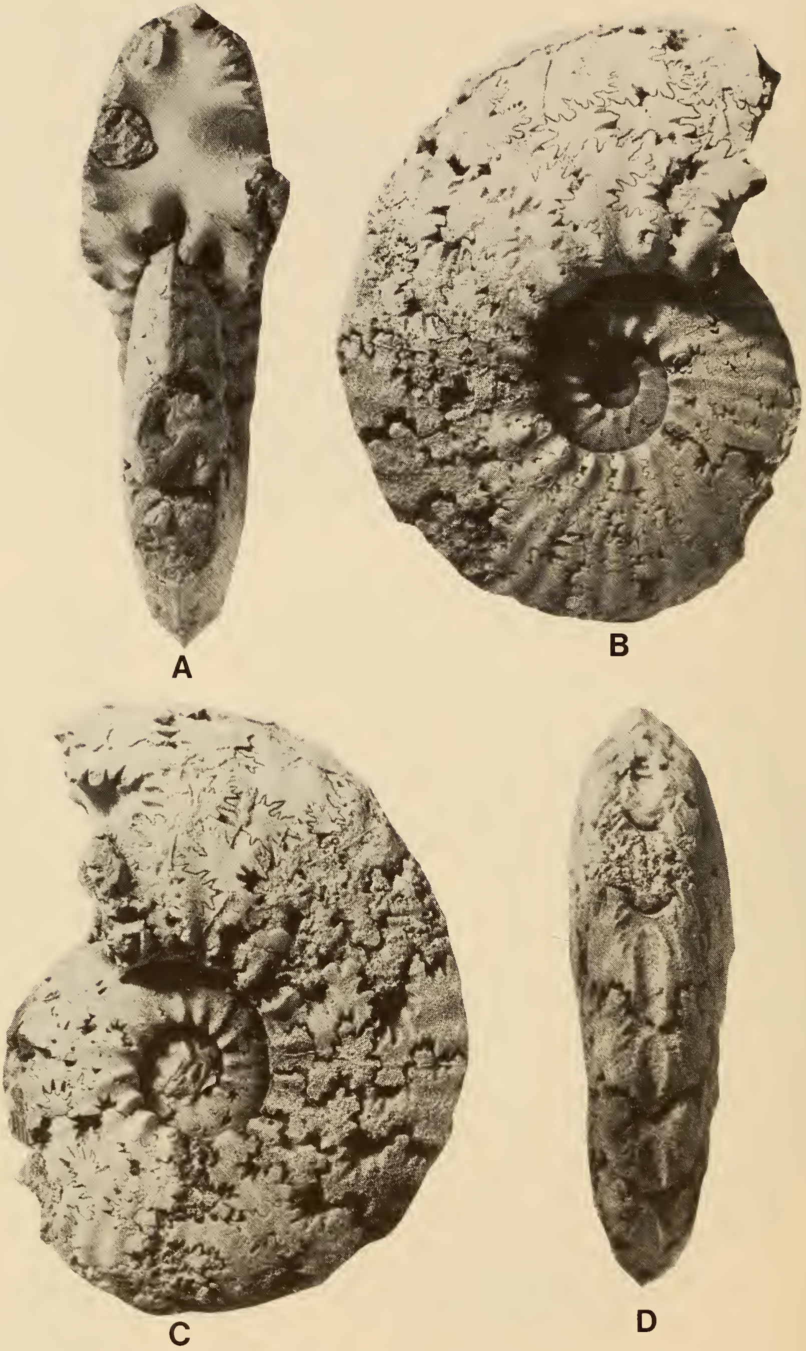

Fig. 3. *Reesidites lornae* (van Hoepen, 1968). Holotype SAS Z1128. ×1.

vations suggest that *Reesidites* may best be treated as a subgenus or even strict synonym of *Barroisiceras*. However, until the type material of *B. haberfellneri* is redescribed and its stratigraphic position clarified, *Reesidites* and *Barroisiceras* are here maintained as separate taxa.

Itwebeoceras van Hoepen, 1968 (type species *Itwebeoceras lornae* van Hoepen, 1968), from the ?Upper Coniacian of Zululand, has the same ornament as *Reesidites*, differing only in detail from that of *R. minimus*. It does not show the same asymmetry of E/L but is here regarded as a synonym. *Buenoceras* Etayo-Serna (1979: 101; type species *B. loboi* Etayo-Serna (1979: 101, pl. 14 (fig. 2), text-figs 9R, U)) from the Coniacian of Colombia is based on a fragment only and may also be a synonym.

Occurrence

Upper Turonian of Japan and Armenia; Coniacian of Colombia, Venezuela, and Zululand.

Reesidites lornae (van Hoepen, 1968)

Figs 2A–C, 3–4.

Itwebeoceras lornae van Hoepen: 1968*a*: 184, pl. 4.

Holotype

By monotypy, SAS Z1128, from the St. Lucia Formation, (Coniacian ?IV), locality 13 of Van Hoepen (1968*a*, 1968*b*) = locality 73 of Kennedy & Klinger (1975).

Dimensions

D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
c. 74,5(100)	21,0(—)	31,5(—)		22,7(—)
46,5(100)	14,1(30,3)	20,0(43,0)	0,71	13,2(28,3)
36,6(100)	11,1(30,3)	16,0(43,7)	0,69	10,0(27,3)

Description

The holotype is a wholly septate internal mould, somewhat corroded on the ventral region of the outer whorl; the estimated maximum diameter is approximately 75 mm.

The smallest diameter at which the specimen can be examined is 17 mm (Fig. 4). At this size the coiling is rather involute, half the previous whorl being covered. The whorl section is compressed (whorl breadth to height ratio is 0,8), with the greatest breadth at the umbilical bullae. The flanks are flattened and convergent, the ventrolateral shoulders narrowly rounded, and the venter fastigiate. There are twelve prominent umbilical bullae per whorl; these give rise to pairs of low, broad prorsiradiate ribs strengthened into an oblique ventrolateral clavus from which they sweep forward across the ventrolateral shoulder, declining as they do so. There is an initially entire siphonal keel

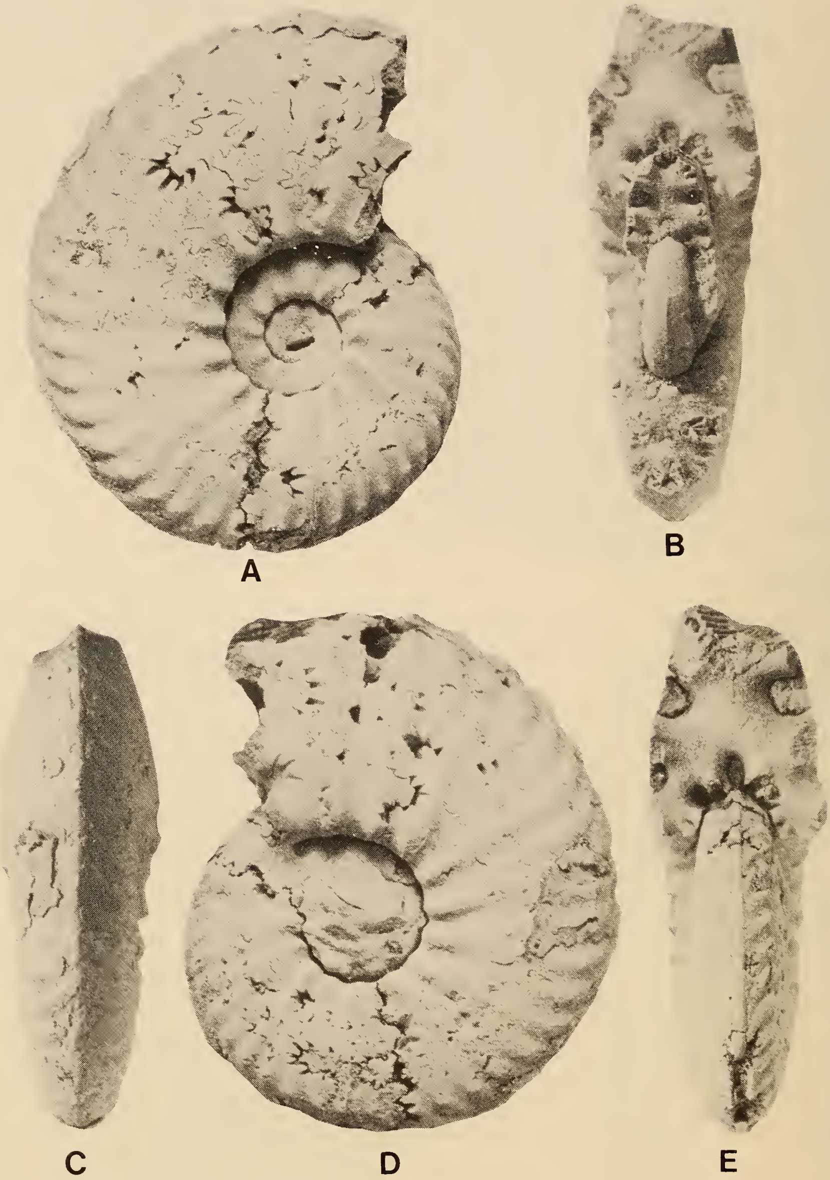

Fig. 4. *Reesidites lornae* (van Hoepen, 1968). Holotype SAS Z1128. ×2.

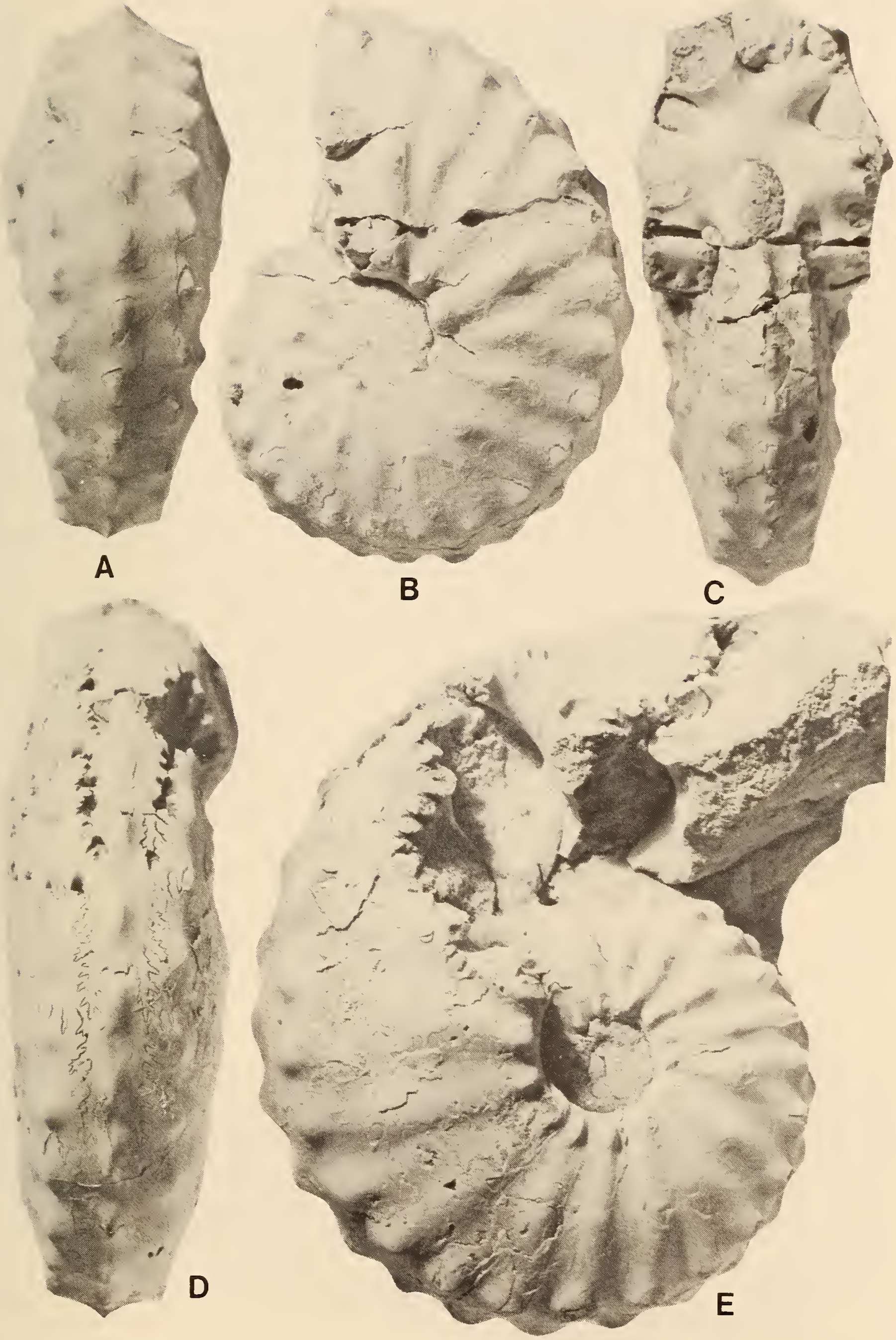

Fig. 5. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–C. A paratype of '*Basseoceras krameri*' van Hoepen, 1968, SAS Z1437. D–E. Another paratype, SAS Z978. All ×1.

Fig. 6. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Holotype of '*Basseoceras krameri*' van Hoepen, 1968, SAS Z935.

flanked by faint, shallow grooves, which subsequently develops low crenulations, each of which corresponds to a rib. As size increases, ribbing and tuberculation becomes increasingly differentiated. At a diameter of 36 mm the coiling has become a little more evolute (umbilicus is 27,3 % of diameter) and higher-whorled (whorl breadth to height ratio of 0,69). There are fifteen medium-sized umbilical bullae per whorl. These give rise to pairs of low, relatively broad, flexuous prorsiradiate ribs that sweep forward across the inner flank, are feebly convex across the mid-flank and feebly concave across the outer flank. Occasional intercalated ribs are inserted around mid-flank and all the ribs develop a small, conical ventrolateral tubercle. These give rise to broad prorsiradiate extensions of the ribs that sweep forward to link with elongate siphonal clavi borne on the siphonal keel. There are thirty-eight ribs per whorl at this diameter, corresponding to a slightly smaller number of ventral clavi.

This style of ornament extends to the greatest diameter preserved where there are seventeen to eighteen umbilical bullae per whorl and a total of forty-two ribs.

The suture line is shown in Fig. 2A–C. Elements are relatively simple and little subdivided, with a broad, slightly asymmetric bifid E/L, narrower bifid L, narrow, slightly asymmetric L/U_2, small U, and broad, simple U_2/U_3.

Discussion

Reesidites lornae resembles *R. minimus* (see Matsumoto 1965: 63, pl. 14 (fig. 1), pl. 15 (figs 1–3), text-figs 34–39) but differs in being more evolute, with stronger bullae, broader whorls, narrower, better differentiated ribs, and an essentially symmetrical rather than asymmetric E/L. *R. elegans* Matsumoto & Inoma (1971: 139, pl. 23 (figs 1–3), text-figs 5–7) is much more delicately and flexuously ribbed, with more secondary ribs. *R. subtuberculatus* (Gerhardt) (1897: 156, pl. 3 (fig. 12)) has far fewer ribs, lacks bullae, and has a broader venter without obvious ribs but rather with striae between ventrolateral and siphonal clavi.

There is a striking similarity between *R. lornae* and '*Schlönbachia (Gauthiericeras)*' *crioceratiformis* Lüthy (1918: 43, pl. 3 (fig. 2)) from the Coniacian of Peru. The outer whorl of the wholly septate holotype of this species uncoils, perhaps due to pathological disturbance of growth, and further material is needed before placing *lornae* in synonymy with *crioceratiformis*.

Occurrence

St. Lucia Formation of Zululand. Precise age unknown but certainly Coniacian and possibly Coniacian IV.

Genus *Forresteria* Reeside, 1932

Type species

Barroisiceras (Forresteria) forresteri Reeside (1932: 17, pl. 5 (figs 2–7)), by the subsequent designation of Wright (1957: L432) = *Acanthoceras (Prionotro-*

Fig. 7. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Slender variants. A–C. SAM–D1187G. D–F. '*Barroisiceras (Harleites) castellense*' Reeside, 1932. The holotype USNM 73758 from the Mancos Shale, some 61 m (200 ft) above the top of the Ferron Sandstone in Sevier County, Utah. G. SAS Z913, large septate fragment. All ×1.

pis) alluaudi Boule, Lemoine & Thévenin (1907: 32, pl. 8 (figs 6–7), text-fig. 17).

Diagnosis

Both small species (adult at 80–100 mm) and large ones (adult at 250 mm) are known. Coiling varies from involute to moderately evolute, the whorls from compressed to depressed. Early whorls bear weak umbilical bullae, strong to weak lateral tubercles or spines linked by primary ribs, the latter giving rise to pairs of weak to strong secondary ribs which, with intercalatories, are linked to variably developed ventrolateral and siphonal clavi. Ornament may be lost at small diameters, with a smooth or feebly ornamented lanceolate or tabulate venter on the body whorl, or persist, with the tubercles declining only at maturity. The suture is simple with a broad E, narrow E/L and L, with large U_2 in many species.

Occurrence

Coniacian of France, Austria, Czechoslovakia, Israel, west Africa, Zululand, Madagascar, Japan, Colombia, Mexico, and the United States (Utah and Wyoming).

Subgenus *Forresteria (Forresteria)* Reeside, 1932

(= ?*Zumpangoceras* Basse, 1947: 144; *Collignonella* van Hoepen, 1957: 350 (*pro Collignoniceras* van Hoepen, 1955: 361), *non* Breistroffer, 1947: unpaged; *Basseoceras* van Hoepen, 1968*b*: 162 (*non* Collignon, 1965: 73); *Eedenoceras* van Hoepen, 1968*b*: 171; *Neokanabiceras* Collignon, 1965: 42).

Diagnosis

Variable, early whorls as in *Forresteria sensu lato*. In compressed variants the umbilical and lateral tubercles are lost at an early growth stage ('*Basseoceras*' van Hoepen) leaving feeble flank ribs, ventral and siphonal clavi, and a high angular whorl section that persists to over 200 mm. These grade into massively whorled hypernodose individuals with persistent ribs and tubercles. The lateral and ventrolateral tubercles fuse in some species, in others they survive separate to the beginning of the body chamber; thereafter tubercles decline and ribs dominate ornament.

Discussion

The type species of *Forresteria (Forresteria)* was based on a single juvenile specimen (see Fig. 14E–H) from the Mancos Shale of Sevier County, Utah, some 61 m (200 ft) above the top of the Ferron Sandstone. Reeside (1932: 17) remarked that it 'seems very close indeed to the form from the Senonian of Diego-Suarez, Madagascar, described by Boule, Lemoine and Thévenin as *Acanthoceras (Prionotropis) alluaudi*, which seems to the writer to be a species

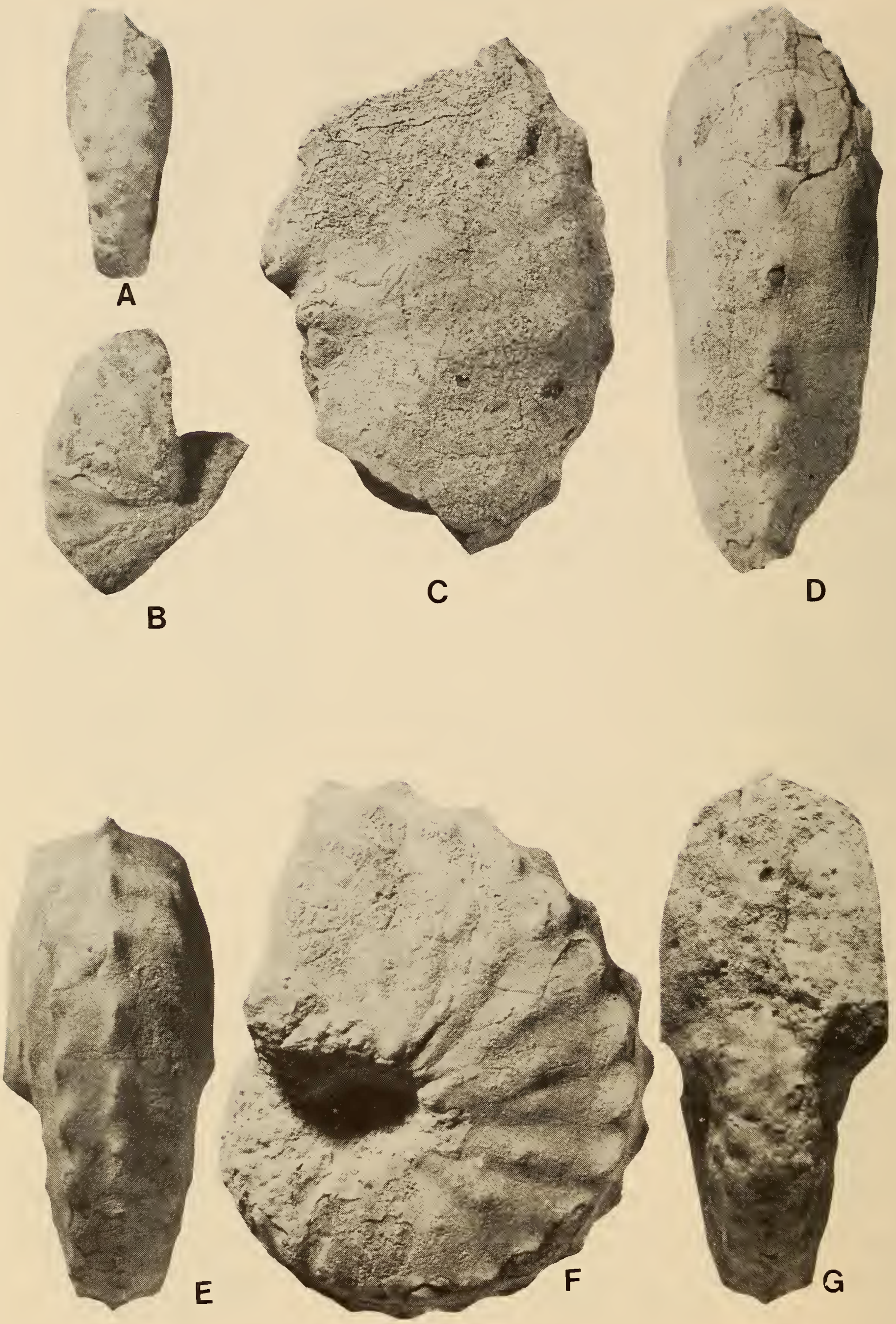

Fig. 8. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. SAM–D1187H. C–D. SAM–D1187F. E–G. SAM–D1187G. All ×1.

of *Barroisiceras. B. forresteri* differs chiefly in its fewer ribs and nodes'. It is believed that the types of *F. (F.) forresteri* and *F. (F.) alluaudi* are so similar that they cannot be separated specifically, as discussed below.

Subsequent accounts of *Forresteria (Forresteria)* have been hampered by the small number of specimens generally available and as a result numerous species, subgenera, and genera have been introduced for a range of ammonites that the large Zululand collections described here suggest belong to no more than a single species.

Initial discussion is restricted to the type material only. The holotype of *F. (F.) forresteri* occurred with a compressed ammonite of similar size and ornament, described by Reeside (1932: 16, pl. 4 (figs 4–8)) as *Barroisiceras (Alstadenites) sevierense* (the holotype, and only specimen described, is illustrated here, Fig. 14A–D), and an even more compressed, involute and feebly ornamented species, also represented by only one specimen and described by Reeside as *Barroisiceras (Harleites) castellense* Reeside (1932: 19, pl. 6 (figs 1–5) (see Fig. 7D–F herein). These three species, referred to three subgenera, in fact represent no more than variable juveniles of a single species, as W. A. Cobban has demonstrated to the authors on the basis of his unpublished new collections. Furthermore, the new American material shows that *Barroisiceras (Forresteria) stantoni* Reeside (1932: 17, pl. 7 (figs 1–7)) is yet a further variant of the same species (Figs 15A–B, 35C–E).

This same variablity of nuclei is confirmed by the South African material described here. Not only do no two nuclei match, but the same range from compressed '*castellense*' forms (e.g. Fig. 7A–C) through feebly ribbed (e.g. Fig. 11A–B) to depressed spinose juveniles (e.g. Fig. 11C–N) can be demonstrated.

Medium sized and large individuals preserve this same wide variation, and the type material of *Basseoceras* van Hoepen, 1968*b* (type species *Basseoceras krameri* van Hoepen, 1968*b*: 164, pl. 7, (fig 2b–g), *non Basseoceras* Collignon, 1965) corresponds to the slender variant with feeble ornament, while *Collignonella* van Hoepen, 1957 (= *Collignoniceras* van Hoepen, 1955, type species *Collignoniceras hammersleyi* van Hoepen, 1955: 361, figs 7–9, *non* Breistroffer 1947) is no more than a large adult of the coarsely ornamented, stout-whorled form (Figs 16A–C, 17A–C).

Size apart, there are no significant or diagnostic differences between this adult and the holotype and only described specimen of *Eedenoceras* van Hoepen, 1968*b* (type species *Eedenoceras multicostatum*, van Hoepen 1968*b*: 171, pl. 12, text-fig. 4b) (re-illustrated here as Figs 12A–B, 13E); it is also a synonym of *Forresteria (Forresteria).*

Although specifically separable from *F. (F.) alluaudi*, the type species of *Neokanabiceras* Collignon, 1965, *N. madagascariense* Collignon (1965: 42, pl. 432 (figs 1784–1786), including var. *ankinatsyense* (fig. 1787)), is a perfectly good *Forresteria (Forresteria)* as is apparent from Wiedmann's recent re-illustration of the type material (in Herm, Kauffman & Wiedmann 1979: 44, pl. 7A–B, text-figs 7D, 8). There are small umbilical bullae linked by primary ribs

Fig. 9A–B. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). BMNH C8333. ×0,7.

Fig. 10. A–B, E–F. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. SAM–D1187L. E–F. SAM–Z167. C–D. *Forresteria (Forresteria) madagascariensis* (Collignon, 1965). SAM–D1187I. All ×1.

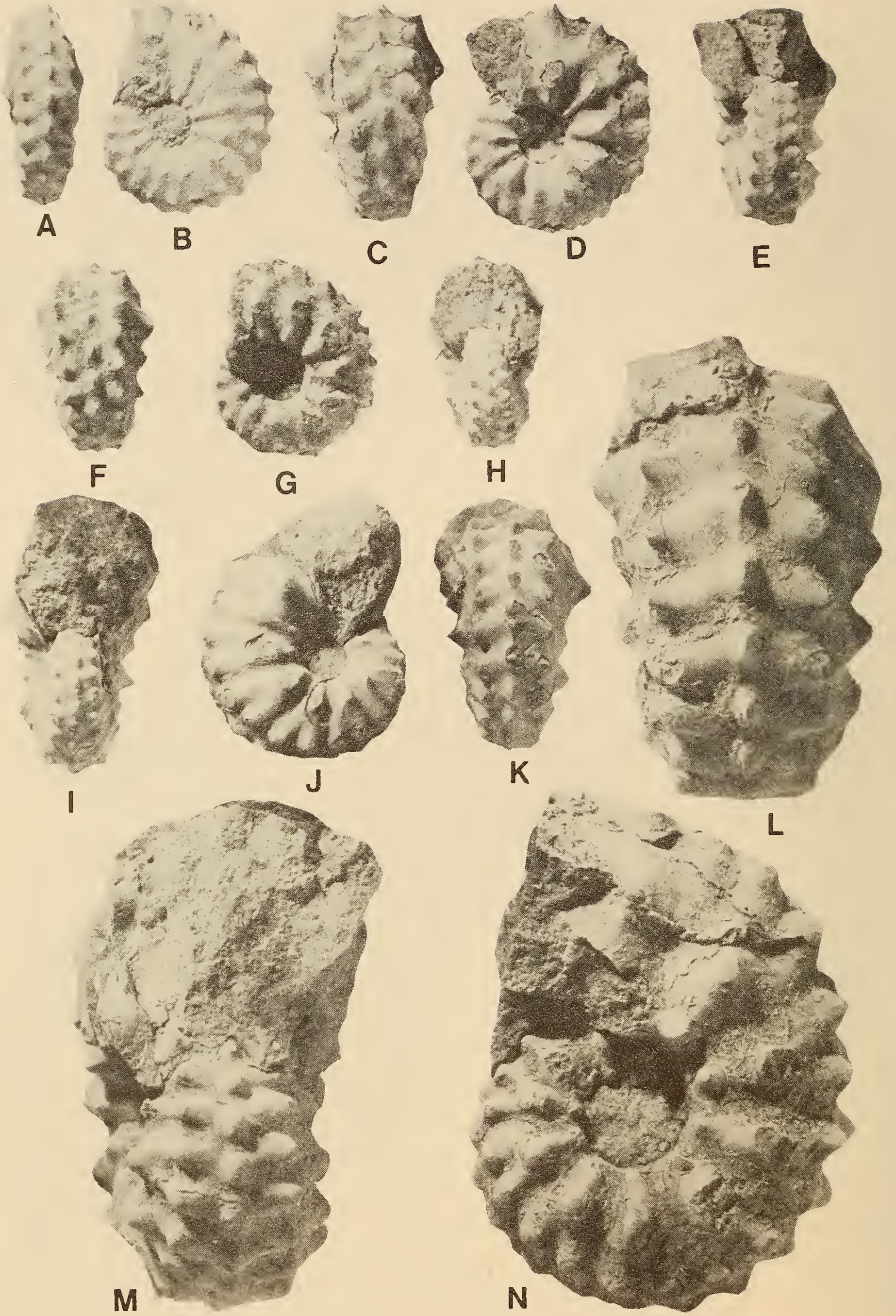

Fig. 11. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. SAS Z2195. C–E. SAS Z1453A. F–H. SAS Z1453B. I–K. SAS Z1438B. L–N. SAS Z946. All ×1.

to massive lateral nodes that give rise to pairs of ribs linking to ventral clavi, exactly as in *Forresteria*; the only difference appears to be that the siphonal clavi are raised on a low siphonal keel. Several specimens of *F. (F.) alluaudi* that have been examined show this feature developed weakly at some stage in ontogeny (e.g. Fig. 13A–B): it is regarded here as no more than a specific difference.

Zumpangoceras Basse, 1947 (type species *Zumpangoceras burckhardti* Basse, 1947: 144) was based on the ammonites described by Burckhardt (1919: 99–108) as *Barroisiceras*, and later illustrated by him (1921, pl. 22 (fig. 16), pl. 23 (figs 1–2), pls 24–25). Basse originally thought this to be a subgenus of *Barroisiceras* and noted the very fine ornament—especially the well-preserved growth striae—and the presence of a lateral tubercle. Etayo-Serna (1979: 99) has designated the original of Burckhardt (1921, pl. 23 (fig. 1)) lectotype of the species. This is a large fragment with lateral (+ ?umbilical) tubercles and more numerous ventral and siphonal clavi linked by ribs and dense growth striae. It appears to be a fragment of a typical *Forresteria (Forresteria)*, so that *Zumpangoceras* also falls into synonymy.

Harleites Reeside, 1932, type species by original designation *Barroisiceras haberfellneri* var. *harlei* de Grossouvre (1894: 56, pl. 2 (figs 2, 7–8)), is based on specimens from the basal Coniacian of the Dordogne, France, now preserved in the collections of the Sorbonne, Paris. This was originally described as a subgenus of *Barroisiceras*, but Basse (1947) noted the presence of a tiny umbilical and inner lateral tubercle on the inner whorls of some of the type material which, taken with the more numerous but feeble ventrolateral and siphonal clavi, led her to treat it as a subgenus of *Forresteria*, a view followed by Wright (1957). Both these authors regarded *Alstadenites* Reeside, 1932 (type species, herein designated, *Ammonites alstadenensis* Schlüter, 1876: 151, pl. 40 (figs 13–16); lectotype, herein designated, the original of Schlüter's pl. 40 (figs 13–16)) as a synonym, a view followed here (indeed, the type species are probably synonymous).

Matsumoto (1969: 327) has, however, afforded *Harleites* full generic status (following Parnes 1964: 21) on the basis of the more involute shell and weak lateral ornament with finer, more numerous and more persistent ventrolateral and siphonal tubercles.

As discussed above, the compressed variants of *Forresteria (Forresteria) alluaudi* in both North America and Zululand are *Harleites*-like in morphology; however, what is the position of the type species?

Re-examination of De Grossouvre's material shows that the large, almost smooth holotype of *H. harlei* (e.g. De Grossouvre 1894, pl. 2 (fig. 2)) shows no trace of tubercles on the earliest part of the outer whorl (in part, perhaps, due to abrasion), but weak umbilical bullae appear on the body chamber (the specimen is septate to a diameter of approximately 60 mm). The same is true of the smaller paratype (De Grossouvre 1894, pl. 2 (fig. 8)), but there are specimens such as that figured in De Grossouvre's pl. 2 (fig. 7) that have an

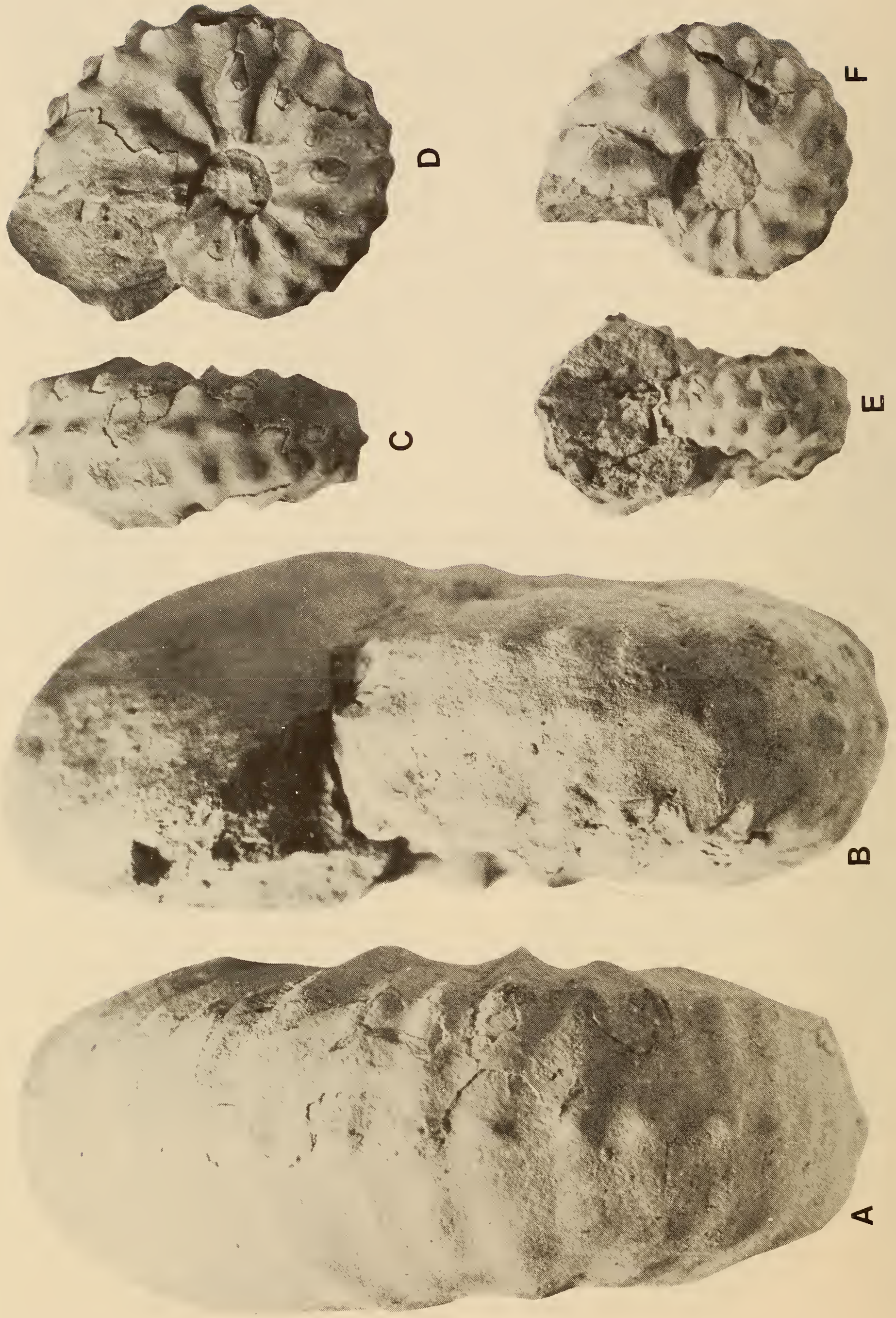

Fig. 12. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. Holotype of '*Eedenoceras multicostatum*' van Hoepen, 1968, SAS Z972. C–D. SAS Z591. E–F. SAS Z591. A–B ×0,75; C–F ×1.

Fig. 13. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. SAS Z987. C–D. SAS Z1438G. E. Holotype of '*Eedenoceras multicostatum*' van Hoepen, 1968, SAS Z972. All ×1.

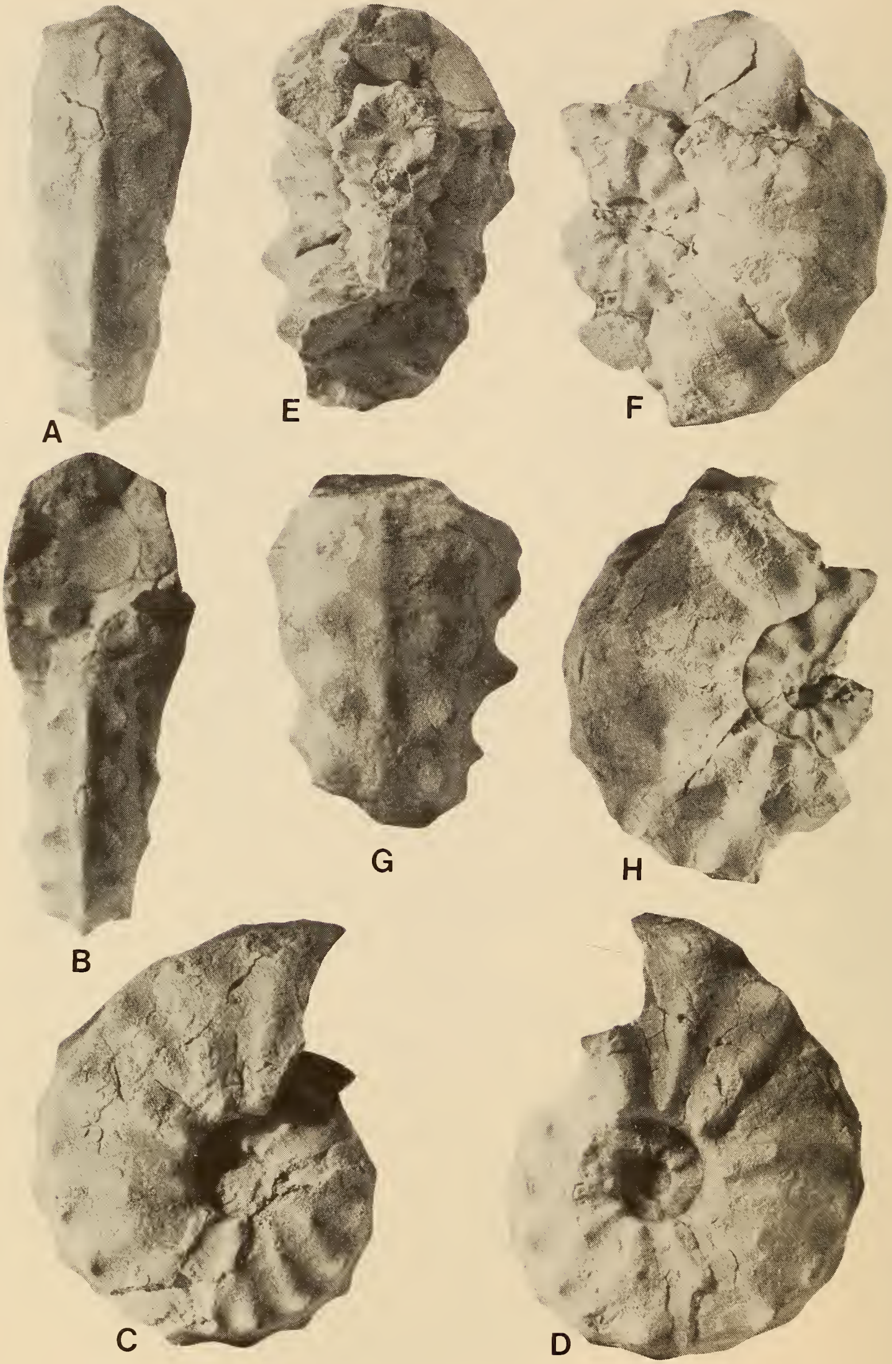

Fig. 14. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–D. Holotype of '*Barroisiceras (Alstadenites) sevierense*' Reeside, 1932, USNM 73756, from the Mancos Shale, some 61 m (200 ft) above the Ferron Sandstone, Sevier County, Utah. E–H. Holotype of '*Barroisiceras (Forresteria) forresteri*' Reeside, 1932, from the same locality and horizon as the original of Figure 14A–D. All ×2.

early stage (up to 25 mm) with tiny umbilical and stronger lateral tubercles before the smooth *harlei* stage. These connect via specimens such as De Grossouvre's var. *alstadenensis* (1894, pl. 2 (fig. 4)) to the variable but strongly ribbed and tuberculate phragmocones of typical *Ammonites petrocoriensis* Coquand (1859: 995) (= *Reesideoceras gallicum* Basse, 1947: 133), the type species of *Reesideoceras* Basse, 1947. The largest French *Harleites* described retain a sharp fastigiate venter with distinct ventral and siphonal clavi to the beginning of the adult body chamber, with renascent umbilical bullae, as noted above. Unfortunately the venter of the holotype of *harlei* is damaged so that the mature venter is not recognizable. According to the figure of Schlüter (1876, pl. 40 (fig. 14)), the lectotype of *H. alstadenensis* shows persistent ventrolateral clavi with a broadly arched flattened venter. In the largest known *Reesideoceras petrocoriensis* (De Grossouvre 1894, pl. 1 (fig. 2)) the siphonal clavi are lost at the beginning of the body chamber and the ventral clavi are raised above a flattened venter, with all tubercles lost on the last quarter whorl.

It is concluded that the types of *Harleites harlei* lie in the same relationship to the type of *Reesideoceras petrocoriense* and other comparably ribbed specimens, as does the holotype of *Harleites castellense* to the holotype of *Forresteria forresteri* (= *alluaudi*) in the United States, or *Basseoceras krameri* to *Forresteria alluaudi* in South Africa. *Reesideoceras* is thus a synonym of *Harleites*, the type species of the latter being *Ammonites petrocoriensis* Coquand, 1859 = *Ammonites alstadenensis* Schlüter, 1876, = *Barroisiceras haberfellneri* de Grossouvre, 1894 (*non* von Hauer) (including varieties *harlei* and *alstadenensis* but not *desmoulinsi* de Grossouvre) = *Reesideoceras gallicum* Basse, 1947.

Harleites (= *Reesideoceras*) is regarded as a subgenus of *Forresteria*, distinguished from *F. (Forresteria)* on the basis of smaller adult size, fusion of mediolateral and umbilical tubercles, and early loss of siphonal clavi leaving a flat or concave venter on the body chamber, on the latter parts of which the ventral clavi may also disappear.

We are not sure how many of the *Harleites* species described by previous authors are referable to the subgenus as interpreted here; Japanese and Madagascan examples may well be no more than compressed and feebly ornamented variants of *F. (Forresteria)*.

Because *F. (Forresteria)* and *F. (Harleites)* have very different geographical distributions the present authors do not believe them to be macro- and microconchs.

Forresteria (Muramotoa) Matsumoto, 1969, type species by original designation *F. (M.) yezoensis* Matsumoto (1969: 317, pl. 42 (figs 1–2), text-figs 8–9) is based on three specimens only from the Coniacian of Hokkaido, Japan. The inner whorls are identical in style and proportions to those of *F. (Forresteria)*, but the ornament is rapidly lost at maturity, leaving a body chamber smooth but for a faintly serrated siphonal ridge. The holotype of the type species is

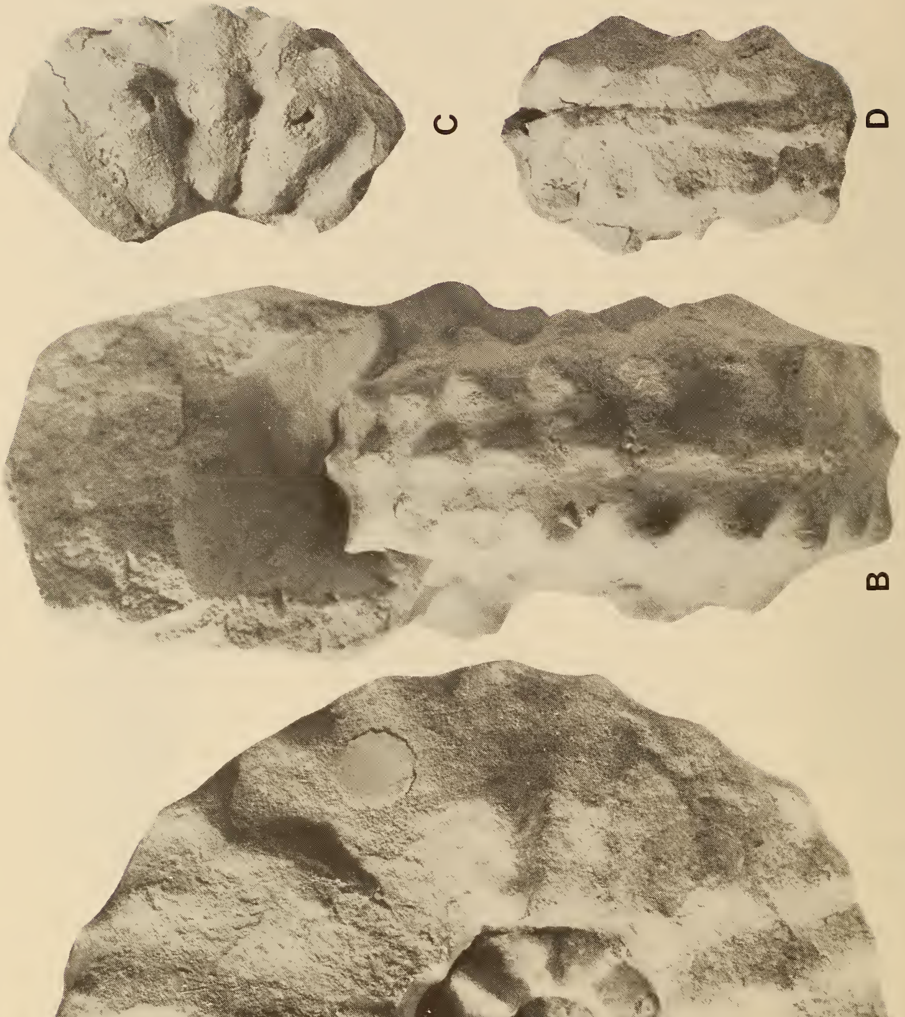

Fig. 15. A–B. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Holotype of '*Barroisiceras (Forresteria) stantoni*' Reeside, 1932, USNM 73761, from the Frontier Formation, south-east of Lander, Wyoming. C–D. *Forresteria (Forresteria) madagascariensis* (Collignon, 1965), SAS Z1187F. All ×1.

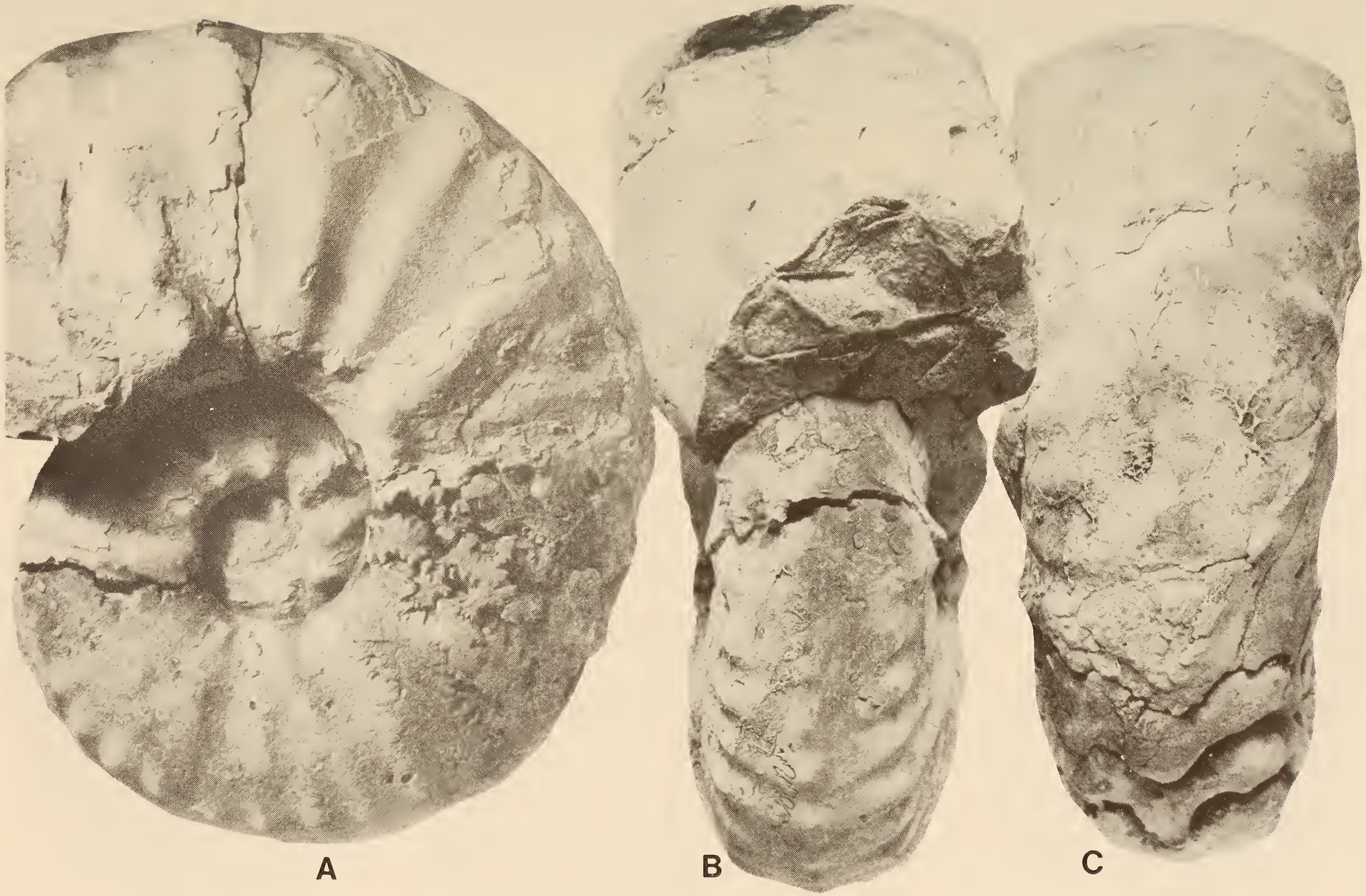

Fig. 16. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Holotype of '*Collignoniceras hammersleyi*' van Hoepen, 1955, SAS Z16. ×0,5.

Fig. 17. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Inner whorls of the holotype of '*Collignoniceras hammersleyi*' van Hoepen, 1955, SAS Z16. ×1.

only 75 mm in diameter and the second Japanese species, *F. (M.) muramotoi* Matsumoto (1969: 320, pl. 43 (fig. 1), text-fig. 11), is equally diminutive.

If adult, *Forresteria (M.) yezoensis* and *F. (M.) muramotoi* may represent a specialized micromorph offshoot of *F. (Forresteria)*. That no such specimens are known outside Japan again suggests them to be micromorph, rather than microconch.

We cannot agree with Matsumoto (1969) that *Basseoceras* van Hoepen, 1968 (*non* Collignon, 1965) is a synonym of *Muramotoa*. The type species *Basseoceras krameri* retains ventrolateral and siphonal clavi to a large size and is simply a feebly ribbed, tuberculate compressed and involute variant of *F. (F.) alluaudi*.

Forresteria (Forresteria) is easily distinguished from genera such as *Barroisiceras* de Grossouvre, 1894 (and subgenera), *Pseudobarroisiceras* Shimizu, 1932, and *Niceforoceras* Basse, 1948, on the basis of the presence of strong lateral tubercles.

Solgerites Reeside, 1932 (= *Piveteauoceras* Basse, 1947) may have lateral tubercles, but the body chamber becomes rounded with persistent siphonal clavi in some, or strong ventrolateral nodes. It could represent a derivative of *F. (Forresteria)* of the *hobsoni* group but, not having good material for study, the position of the genus is unclear to the present authors.

Occurrence

Forresteria (Forresteria) is known from the Coniacian of Israel, west Africa, Zululand, Madagascar, Japan, Mexico, Colombia, and the United States (Utah, Colorado and Wyoming).

Forresteria (Forresteria) alluaudi (Boule, Lemoine & Thévenin, 1907)

Figs 5–9, 10A–B, E–F, 11–14, 15A–B, 16–31, 33–34, 35C–E, 40D–E

Acanthoceras (Prionotropis) alluaudi Boule, Lemoine & Thévenin, 1907: 12, pl. 1 (figs 6–7), text-fig. 17.

Prionotropis alluaudi Boule, Lemoine & Thévenin, 1907: Lisson, 1908: 17, pl. 17. Brüggen, 1910: 772. Basse, 1935: 90. Hourcq, 1936: 6.

Barroisiceras (Forresteria) alluaudi (Boule, Lemoine & Thévenin): Reeside, 1932: 12, 14. Benavides-Caceres, 1956: 478, pl. 61 (fig. 1).

Barroisiceras (Alstadenites) sevierense Reeside, 1932: 16, pl. 4 (figs 4–8).

Barroisiceras (Forresteria) forresteri Reeside, 1932: 17, pl. 5 (figs 2–7).

Barroisiceras (Forresteria) stantoni Reeside, 1932: 17, pl. 7 (figs 1–7), pl. 8 (figs 1–3), pl. 9 (fig. 1).

Barroisiceras (Harleites) castellense Reeside, 1932: 19, pl. 6 (figs 1–5).

Mortoniceras vinassai Venzo, 1935: 88, pl. 7 (fig. 12).

Forresteria alluaudi blt. [*sic*]: Basse, 1947: 128, pl. 8 (fig. 3), pl. 9, (fig. 2).

Forresteria sevierense Reeside: Basse, 1947: 131.

Harleites (?) *castellensis* Reeside: Basse, 1947: 140.

Collignoniceras hammersleyi van Hoepen, 1955: 361, figs 7–9.

Collignoniceras peregrinator van Hoepen, 1955: 364, figs 10–11.

Forresteria (Forresteria) alluaudi Boule, Lemoine & Thévenin: Wright, 1957: L432, fig. 551 (2).

? Forresteria cf. *alluaudi* (BLT) [*sic*]: Parnes, 1964: 23, pl. 2 (figs 7–8).

Forresteria alluaudi B.L.Th [*sic*]: Collignon, 1965: 76, pl. 448 (fig. 1828).

Forresteria razafiniparyi Collignon, 1965: 78, pl. 449 (figs 1829–1831).
Forresteria costata Collignon, 1965: 80, pl. 450 (figs 1833–1834).
Basseoceras krameri van Hoepen, 1968: 164, pl. 7, text-fig. 2b–g.
Forresteria hammersleyi (van Hoepen, 1955): van Hoepen, 1968: 166, pl. 8.
Forresteria vandenbergi van Hoepen, 1968: 167, pl. 9, text-fig. 3a–b.
Forresteria itwebae van Hoepen, 1968: 169, pl. 10, text-fig. 3c.
Forresteria reymenti van Hoepen, 1968: 169, pl. 9, text-figs 3d–e, 4a.
Eedenoceras multicostatum van Hoepen, 1968: 171, pl. 12, text-fig. 4b.
Forresteria (Forresteria) alluaudi (Boule, Lemoine & Thévenin, 1907): Matsumoto, 1969: 308, pl. 40 (figs 1–4), text-figs 5–7. González-Arreole, 1977: 171, text-fig. 2f–h.
Forresteria (Forresteria) armata Matsumoto, 1969: 313, pl. 41 (fig. 1), text-fig. 8.
? Zumpangoceras ospinai Etayo-Serna, 1979: 99, pl. 14 (fig. 8), text-fig. 9O–P.

Types

The smaller of the two specimens from Madagascar figured by Boule, Lemoine & Thévenin (1907, pl. 1 (fig. 7), text-fig. 17), is here designated lectotype of the species.

Material

More than a hundred specimens in the SAM, SAS, and BMNH collections, from the St. Lucia Formation, Coniacian II of localities 10, 13, 92, 93, and 145, including the holotypes of *Collignoniceras hammersleyi* van Hoepen, 1955, *C. peregrinator* van Hoepen, 1955, the holotype and syntypes of *Basseoceras krameri* van Hoepen, 1968*b*, the holotype of *Forresteria vandenbergi* van Hoepen, 1968*b*, *F. itwebae* van Hoepen, 1968*b*, *F. reymenti* van Hoepen, 1968*b*, and *Eedenoceras multicostatum* van Hoepen, 1968*b*.

Dimensions

		D	*Wb*	*Wh*	*Wb* : *Wh*	*U*	ut^1	vt^2
SAS Z935, holotype of *B. krameri*	*c*	107,5(100)	41,2(26,1)	54,9(51,1)	0,75	17,8(16,6)		
SAS Z167	*c*	89,3(100)	37,5(42,0)	43,7(48,9)	0,86	19,5(21,8)	?15	23–24
SAS Z1429	*c*	81,2(100)	35,5(43,7)	37,8(46,6)	0,94	17,9(22,0)	12	24–25
SAS Z1437	*c*	74,2(100)	30,7(41,5)	34,6(46,6)	0,89	13,8(18,6)	12	25
	ic	74,2(100)	29,3(39,4)	32,2(43,4)	0,91			
SAS Z978	*c*	93,5(100)	— (—)	45,0(48,1)	—	18,9(20,0)	13/14	26/27
SAS Z987	*c*	43,0(100)	20,8(48,4)	20,2(47,0)	1,03	9,6(22,3)	9	19
	ic		18,0(41,9)	18,5(43,0)	0,97			
SAS Z591		45,4(100)	21,6(47,6)	21,0(47,6)	1,0	10,6(23,3)	13	?23
			18,2(40,1)	19,8(43,6)	0,92			
SAS 1773	*c*	51,3(100)	— (—)	23,0(44,8)	—	13,5(26,3)	—	—
	ic		— (—)	22,3(43,5)	—			
SAS Z1583, larger specimen	*c*	44,0(100)	24,0(54,5)	20,6(46,8)	1,16	10,9(24,8)	12	—
	ic		21,4(48,6)	17,9(46,7)	1,20			
SAS Z513	*c*	51,5(100)	33,2(64,5)	23,5(45,6)	1,41	15,3(29,7)	12/13	21/22
	ic		27,7(53,8)	20,2(39,2)	1,37			
SAS Z514	*c*	59,7(100)	36,3(60,8)	26,5(44,4)	1,37	18,3(32,6)	13	—
	ic		31,4(52,6)	23,0(38,5)	1,36			
SAS Z7124	*c*	92,0(100)	51,0(55,4)	42,5(46,2)	1,2	24,5(26,6)	—	—
	ic		41,5(45,1)	40,3(43,8)				
SAS Z1687	*c*	103,0(100)	66,7(64,7)	50,0(48,5)	1,33	31,5(30,6)	9	22
	ic		54,0(52,4)	— (—)				
SAS Z922 holotype of *F. reymenti*	*c*	110,0(100)	— (—)	52,5(47,7)		27,5(25,0)	10	24
	ic		— (—)	50,0(45,5)				
	c	87,3(100)	60,5(69,3)	46,3(53,0)	1,31	23,0(26,3)	—	—
	ic		50,0(57,3)	42,0(48,1)	1,19			

ut^1=umbilical tubercles; vt^2=ventral tubercles

		D	*Wb*	*Wh*	*Wb* : *Wh*	*U*	*ut*[1]	*vt*[2]
SAS Z923	*c*	109,0(100)	39,5(36,2)	50,3(46,1)	0,79	27,5(25,2)	14	26/27
	ic		38,0(34,9)	49,3(45,2)	0,77			
	c	83,5(100)	39,5(47,3)	38,5(46,1)	1,03	19,6(23,4)	—	—
	ic		36,3(43,5)	36,3(43,5)	1,00			
	c	— (—)	30,8(—)	27,5(—)	1,12			
	ic		26,5(—)	25,3(—)	1,05			
SAM–D1187N	*c*	99,0(100)	41,0(41,4)	43,3(43,7)	0,95	28,0(28,3)	9/10	—
	ic		39.2(39.6)	40,5(40,9)	0,97			
SAS Z972 holotype of *E. multicostatum*	*c*	140,0(—)	— (—)	64,5(46,0)		36,5(26,1)	13	—
	ic		— (—)	61,5(43,9)				
SAS Z16 holotype of *F. hammersleyi*	*c*	106,5(100)	60,0(56,3)	52,3(49,1)	1,15	28,5(26,8)	11	24
	ic		56,0(52,6)	48,5(45,5)	1,15			
SAS Z16	*c*	150,0(100)	76,5(51,0)	— (—)	—	39,0(26,0)	12	28
	ic		70,5(47,0)	— (—)	—			
	c	230,0(—)	106,0(46,0)	102,0(44,3)	1,04	65,0(28,2)	13/14	32/33
	ic		96,0(41,7)	100,0(43,5)	0,96			

ut[1] = umbilical tubercles; *vt*[2] = ventral tubercles

Description

Previous accounts of *Forresteria (Forresteria) alluaudi* and other species have been based on small numbers of specimens, and a number of species are based on single specimens. Over a hundred specimens were available, all from a narrow stratigraphic interval and, in a number of cases, associated specimens from single lines of concretions. These show that *F. (F.) alluaudi* is variable in the extreme, and that there is widespread co-variance between depth and relative diameter of umbilicus, whorl height, and strength and rate of disappearance of ornament. On the basis of this material the authors place in synonymy all the previously named South African *Forresteria*, all those described from Madagascar (except *F. (F.) madagascariensis* previously referred to *Neokanabiceras*), plus a number of other Japanese and North American forms.

The compressed, involute, feebly ornamented members of the species are represented by specimens formerly referred to as *Basseoceras krameri* van Hoepen. All specimens studied here are wholly septate juveniles. The smallest specimen seen is SAS Z2195 (Fig. 11A–B), which retains some body chamber and has about twelve primary ribs per whorl, corresponding to twenty-two ventral clavi. The whorl section is compressed with a breadth to height ratio of 0,72, the greatest breadth being at the mid-lateral tubercle. This is linked to SAS Z249, which still retains a full complement of ribs and tubercles at a diameter of 61,2 mm.

SAS Z1429 is somewhat stouter, with a breadth to height ratio of 0,87 at a diameter of 82 mm. There are thirteen to fourteen umbilical bullae at this diameter, and twenty-four ventral and siphonal clavi. The flank ornament is beginning to decline, with the lateral tubercle represented by a slight strengthening of the ribs only from about 55 mm onwards.

The holotype of *Basseoceras krameri*, SAS Z935 (Fig. 6), retains the lateral tubercle and feeble ribs at the smallest diameter visible, being only a little more compressed than Z1429. It is wholly septate and so worn that the

Fig. 18. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Inner whorls of stout variant, SAS Z1687. ×1.

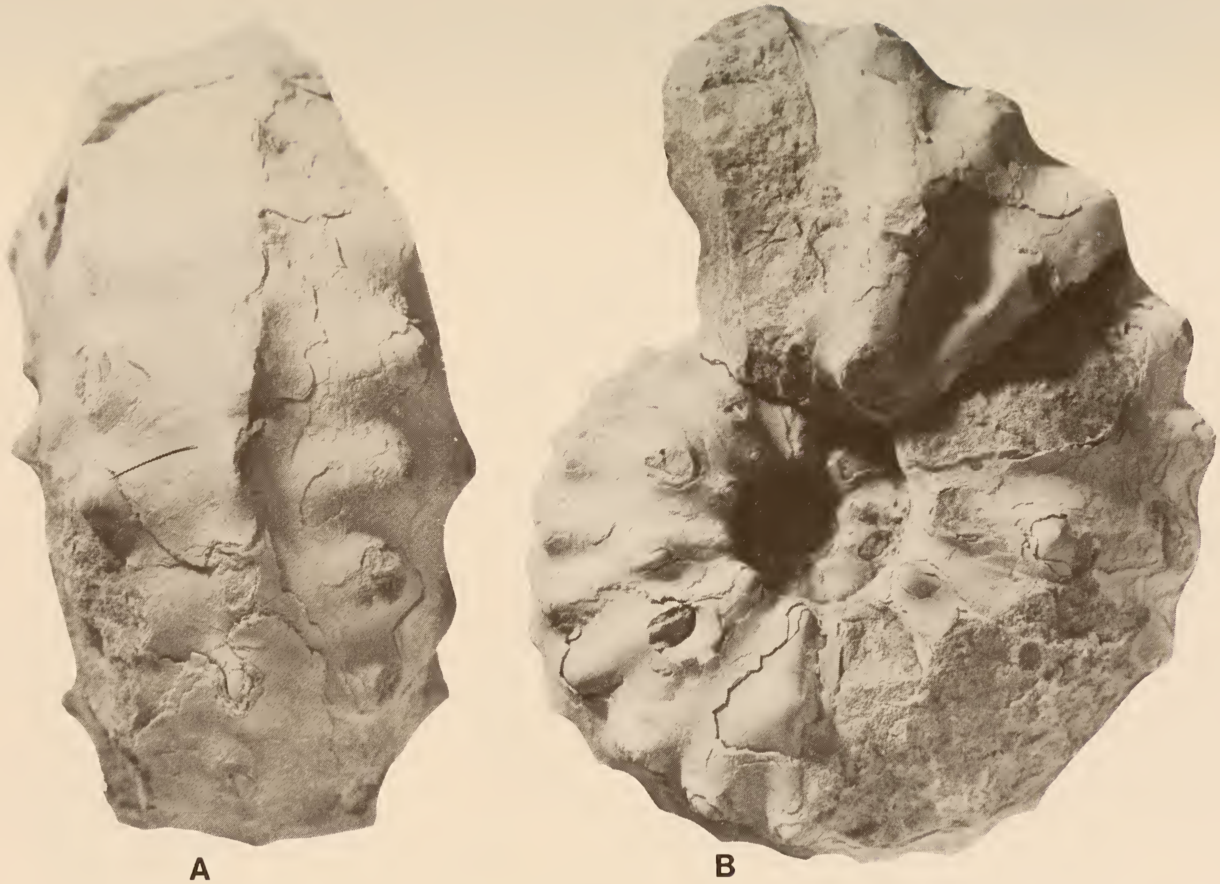

Fig. 19. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Holotype of '*Forresteria reymenti*' van Hoepen, 1968, SAS Z922. ×1.

Fig. 20. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Holotype of '*Forresteria armata*' Matsumoto, 1969, from the Ikushumbets area of Hokkaido, Kyūshū University Collections H 5621. ×1.

ornament is artificially subdued. Umbilical bullae, ribs, and ventral and siphonal clavi are retained throughout, however, and lateral tubercles might well have originally survived to a larger diameter than at present. This is certainly the case in SAS Z913, a very large, wholly septate fragment with a whorl height of 65 mm that still retains low, broad ribs and subdued mid-laterals (Figure 7G).

Amongst other individuals that are relatively compressed is the figured (Van Hoepen 1968*b*, pl. 6) paratype of *Basseoceras krameri*, SAS Z1437 (Fig. 5A–C), which is strongly ribbed with distinct tubercles to a diameter of 75 mm (costal whorl breadth to height ratio 0,87; intercostal 0,79). SAS Z978 is a rather more evolute specimen, with U = 21 per cent as opposed to 16,6 per cent in the holotype. It is especially well preserved (Fig. 5D–E), retaining aragonitic shell, and is wholly septate. The lateral tubercles are distinct to a diameter of about 60 mm but decline thereafter. SAS Z949 is similar, with stronger decoration to the inner whorls but a similar decline beyond 60–65 mm diameter.

The authors have many small specimens of up to about 50–60 mm diameter that show a progressive increase in strength of ornament with increasing whorl inflation, e.g. SAS Z591 (Fig. 12C–D).

Similar transitions at a somewhat greater diameter—up to 120 mm—link SAS Z976 (Fig. 26), Z969 (Fig. 27), and Z922 (Fig. 19, the holotype of *Forresteria reymenti*).

Within this range of ornament and size fall the types of *Forresteria alluaudi* (Boule, Lemoine & Thévenin), *F. forresteri* (Reeside), *F. razafiniparyi* Collignon and *F. costata* Collignon, all of which can be matched in this series.

There are also specimens that show sparse ribbing—SAS Z1782 (Fig. 21) and the holotype of *F. peregrinator* (van Hoepen) (Fig. 25A–B). Although at first sight appearing distinct, they are simply a further variant of the species and these small individuals match the inner whorls of the large specimens described as *F. vandenbergi* van Hoepen (Fig. 23A–B) and *F. itwebae* van Hoepen (Figs 31, 40D–E). *F. armata* Matsumoto (Fig. 20) is an individual of this type, and also probably a synonym.

With increasing diameter, changes in ornament suggesting the approach of maturity are shown by a number of specimens. SAS Z979 (Fig. 29) and SAS Z923 (Fig. 28) have inner whorls only moderately inflated, ribbed, and tuberculated up to a diameter of about 65 mm, whereafter the whorls become more evolute, lateral tubercles decline, and ribs crowd. This to a degree follows the changes seen in feebly ribbed *Basseoceras krameri* variants. The more inflated holotype of *Eedenoceras multicostatum* van Hoepen (Figs 12A–B, 13E) shows typical strong, inflated inner whorls to a diameter of about 70–80 mm; thereafter the lateral tubercles decline and one or two shorter intercalated ribs become prominent on the last half whorl. This is essentially what is shown by SAS Z923 but with more intercalatories. This is regarded as individual body chamber variation in a small adult.

Contrasting with these specimens that appear adult at 120–160 mm are specimens that remain septate to beyond this diameter; this applies to feebly

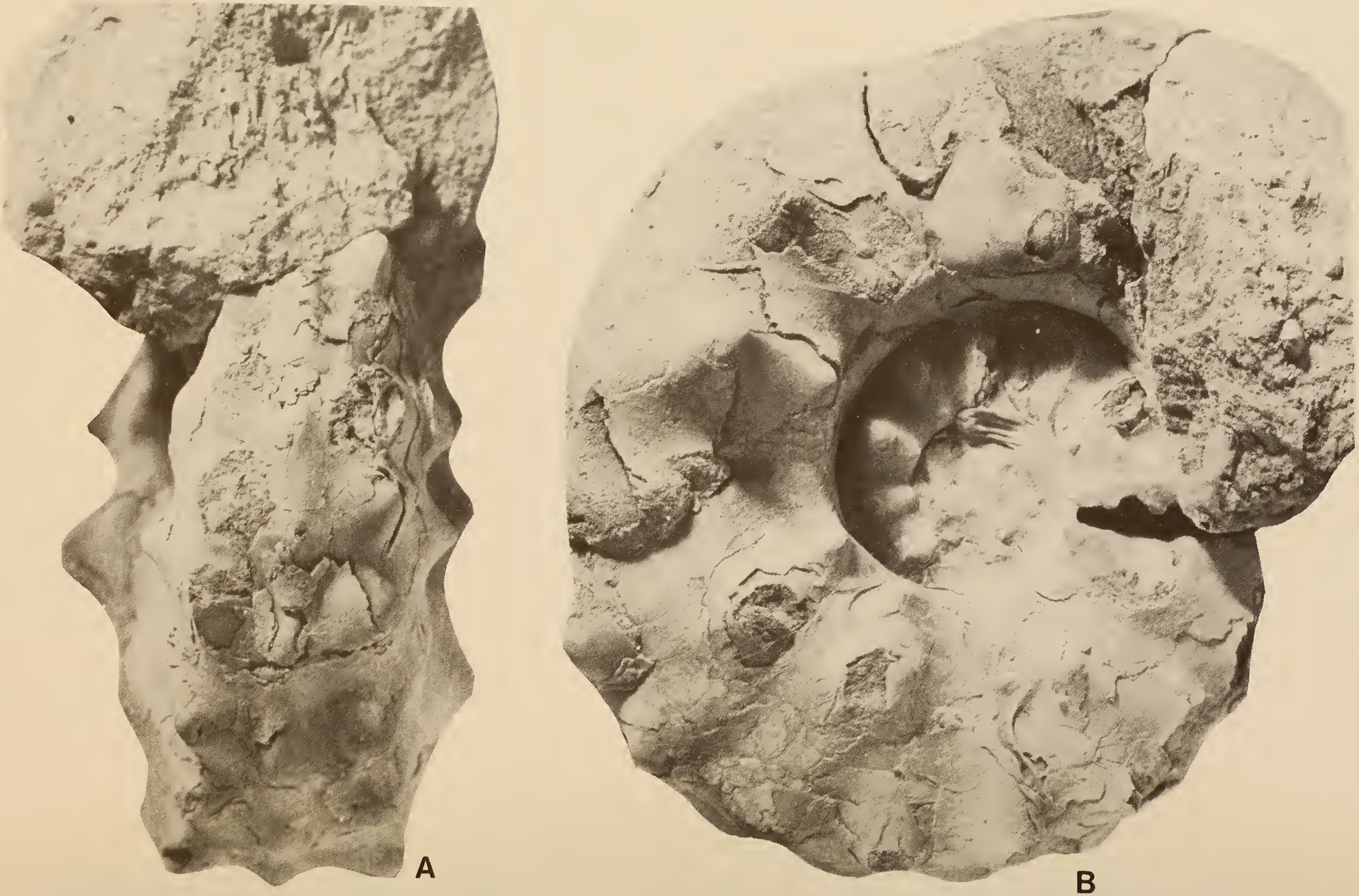

Fig. 21. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). SAS Z1782. × 1.

ornamented specimens, e.g. SAS Z913, rather compressed and sparsely ribbed individuals, e.g. the type of *Forresteria vandenbergi*, and more inflated and strongly decorated individuals such as SAS Z1981. The most complete of these large adults is the holotype of *F. hammersleyi* (van Hoepen) (Figs 16–17). This shows intercalated ribs, singly or in pairs, as in the smaller adult holotype of '*Eedenoceras*' *multicostatum*, but with traces of the lateral tubercle to the end of the clearly adult body chamber at almost 230 mm diameter.

The sutures are variable, depending on whorl section and position relative to ribs and tubercles, as shown in Figures 33–34.

Discussion

The description given above indicates that all the species originally described from Zululand (*Basseoceras krameri* van Hoepen, *Forresteria hammersleyi*, (van Hoepen), *F. peregrinator* (van Hoepen), *F. vinassai* (Venzo), *F. vandenbergi* van Hoepen, *F. itwebae* van Hoepen, *F. reymenti* van Hoepen, *Eedenoceras multicostatum* van Hoepen, and the Madagascan *Forresteria razafiniparyi* Collignon, *F. costata* Collignon, and *F. alluaudi* (Boule, Lemoine and Thévenin)) can be matched in the present collection and that they are to be treated as no more than variants of a single, apparently dimorphic species, for which the name *F. (F.) alluaudi* has priority. It has been recognized that the North American *F. forresteri* Reeside (1932: 17, pl. 5 (figs 2–7)) (Fig. 14E–H) was also a synonym of *F. (F.) alluaudi*, and this is confirmed by the Zululand material. *F. forresteri* co-occurs with *Barroisiceras (Harleites) castellense* Reeside (1932: 19, pl. 6 (figs 1–5)) (Fig. 7D–F herein) which is a very compressed variant of this species.

Forresteria stantoni Reeside (1932: 17, pl. 7 (figs 1–7); pl. 8 (figs 1–3), pl. 9 (fig. 1)) (Fig. 35C–E herein) is no more than a variant of *F. alluaudi* as is *Barroisiceras (Alstadenites) sevierense* Reeside (1932: 16, pl. 4 (figs 4–8)) (Fig. 14A–D herein). In contrast, *Forresteria hobsoni* Reeside (1932: 18, pl. 9 (figs 2–4), pl. 10 (figs 1–2)) (Fig. 35A–B herein) is a quite distinct species, discussed further below. It is more evolute and slender-whorled, and shows a development of sparse ventrolateral horns developed by fusion of lateral and ventrolateral tubercles, amongst other differences. *Neokanabiceras madagascariensis* Collignon (1965: 42, pl. 432 (figs 1784–1787)) is regarded here as a distinct species of *Forresteria* only, rather than meriting generic separation. It differs from the variable *F. alluaudi* in being more slowly expanding and in the development of very strong horns from the lateral tubercle with increasing diameter. The horns bear rounded ribs that link them to pairs of rather small transverse or oblique ventrolateral tubercles. The siphonal clavi are borne on a low ridge. It is thus closer to *F. hobsoni*.

Forresteria nwalii (Reyment) (= *Barroisiceras nwalii* Reyment, in Offodile & Reyment 1976: 61, fig. 14a–b), from the Coniacian of Nigeria, the holotype and only known specimen, refigured here as Figure 39, is also a distinct species allied to *F. madagascariensis*. It differs very obviously from

Fig. 22. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). SAS Z1456. × 1.

Fig. 23. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. Holotype of '*Forresteria vandenbergi*' van Hoepen, 1968. SAS Z70. ×0,75. C–D. SAS Z513. ×1.

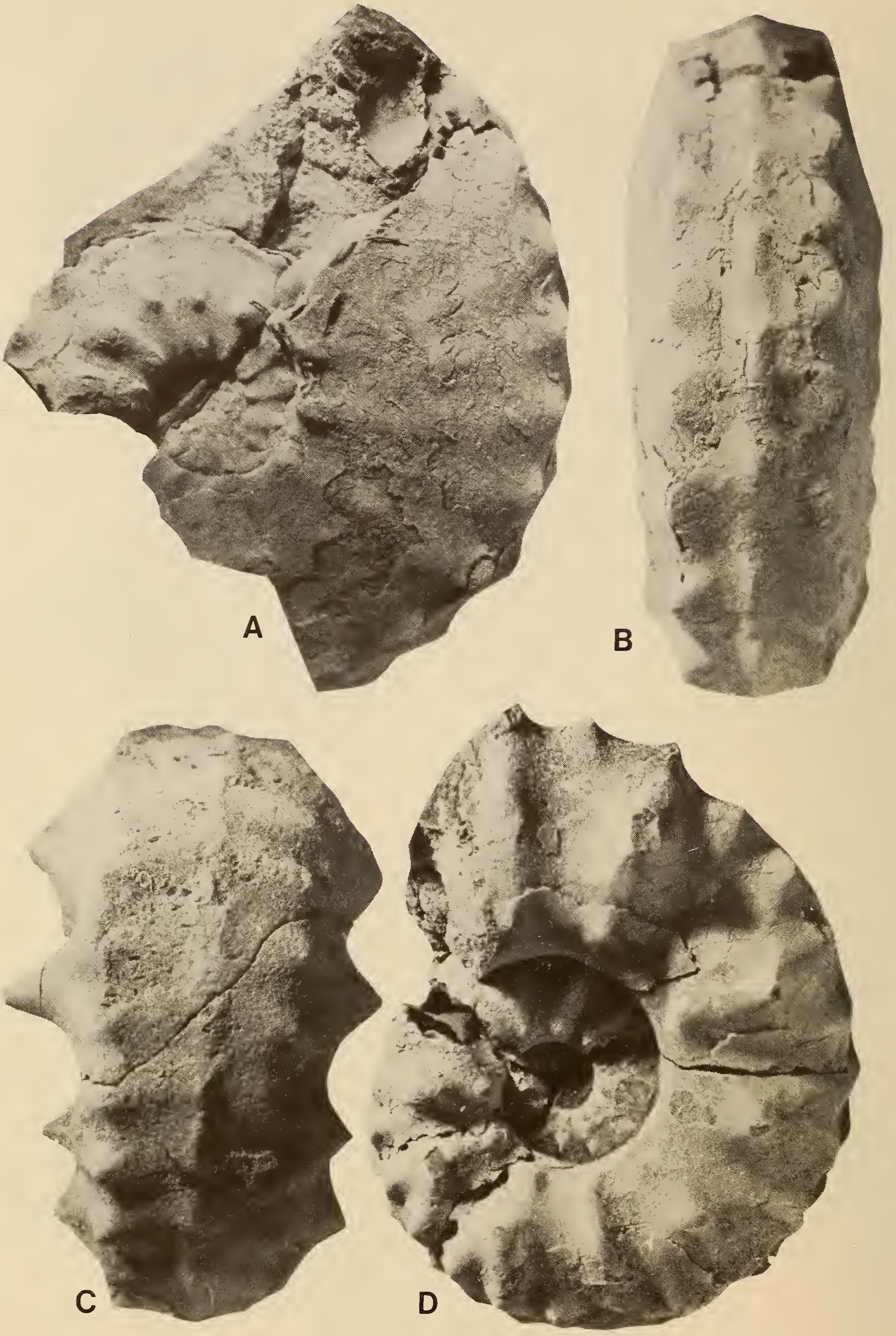

Fig. 24. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. SAS Z949. C–D. SAS H196/2. All ×1.

F. (F.) alluaudi in developing massive pinched lateral horns that bear looped ribs connecting to ventral clavi and lacks an umbilical bulla (whether the lateral horn develops from the fusion of an umbilical bulla and lateral tubercle on the inner whorls or represents merely the outward migration and accentuation of the umbilical bulla above is not clear, due to artificial carving of ribs on the inner whorl of the type specimen). *F. serrata* Reyment (1955: 69, pl. 15 fig. 3a–b)), from the Coniacian Awgu-Ndeaboh Shales near Enugu, Nigeria, is known from the holotype only, a juvenile 36,5 mm in diameter. The flanks are flattened and subparallel, with a rounded fastigiate venter. Weak umbilical bullae give rise to narrow primary ribs that develop into a bullate tubercle on the ventrolateral shoulder, where they are joined by one or two non-tuberculate intercalatories. The ribs terminate in a blunt ventrolateral bulla separated by a smooth zone from a row of weak siphonal clavi. This ornament is very different from that of most *F. (Forresteria)* species, and is transitional towards *Yabeiceras*.

Reyment (1958: 68, pl. 6 (fig. 1)) referred *Reesideoceras camerounense* Basse, 1947 (= *Barroisiceras haberfellneri* von Hauer var. *alstadenensis* (Schlüter) de Grossouvre of Solger, 1904: 170, pl. 5 (fig. 6), text-figs 56–57) to *Forresteria (Forresteria)*. It appears rather to be a *F. (Reesideoceras)*. The *Forresteria* cf. *allaudi* [*sic*] of Parnes (1964: 23, pl. 2 (figs 7–8)) may belong here or to *F. (F.) peruanum* (Brüggen) (see below); it is crushed. *F. (F.) peruana* (= *Gauthiericeras margae* var. *peruanum* Brüggen, 1910: 720, pl. 27 (fig. 3) = *F. (F.) bassae* Benavides-Cacéres (1956: 477, pl. 58 (fig. 5)) from the Coniacian of South America appears to be a distinctive compressed species, perhaps closer to *F. (F.) hobsoni*. The best representation of this species is by Lüthy (1918: 41, pl. 1 (fig. 2a–b)). It does not find a match in the material here referred to *F. (F.) alluaudi*.

Zumpangoceras ospinai Etayo-Serna (1979: 90, pl. 74 (fig. 8), text-figs 9O, 9P) from Colombia may be a synonym of *F. (F.) alluaudi* but is figured in side view only. *F. (F.) armata* Matsumoto (1969: 313, pl. 41, (fig. 1), text-fig 8) is a clear synonym, as discussed above.

Occurrence

This species characterizes the Coniacian in many areas of the world and is known from Zululand, Madagascar, Japan, Mexico, the United States Western Interior, ? Colombia, Peru, and perhaps Israel. In South Africa it is restricted to Coniacian II of Kennedy & Klinger (1975).

Forresteria (Forresteria) cf. *hobsoni* (Reeside, 1932)

Fig. 32

Compare

Barroisiceras (Forresteria) hobsoni Reeside, 1932: 18, pl. 9 (figs 2–4), pl. 10 (figs 1–2).

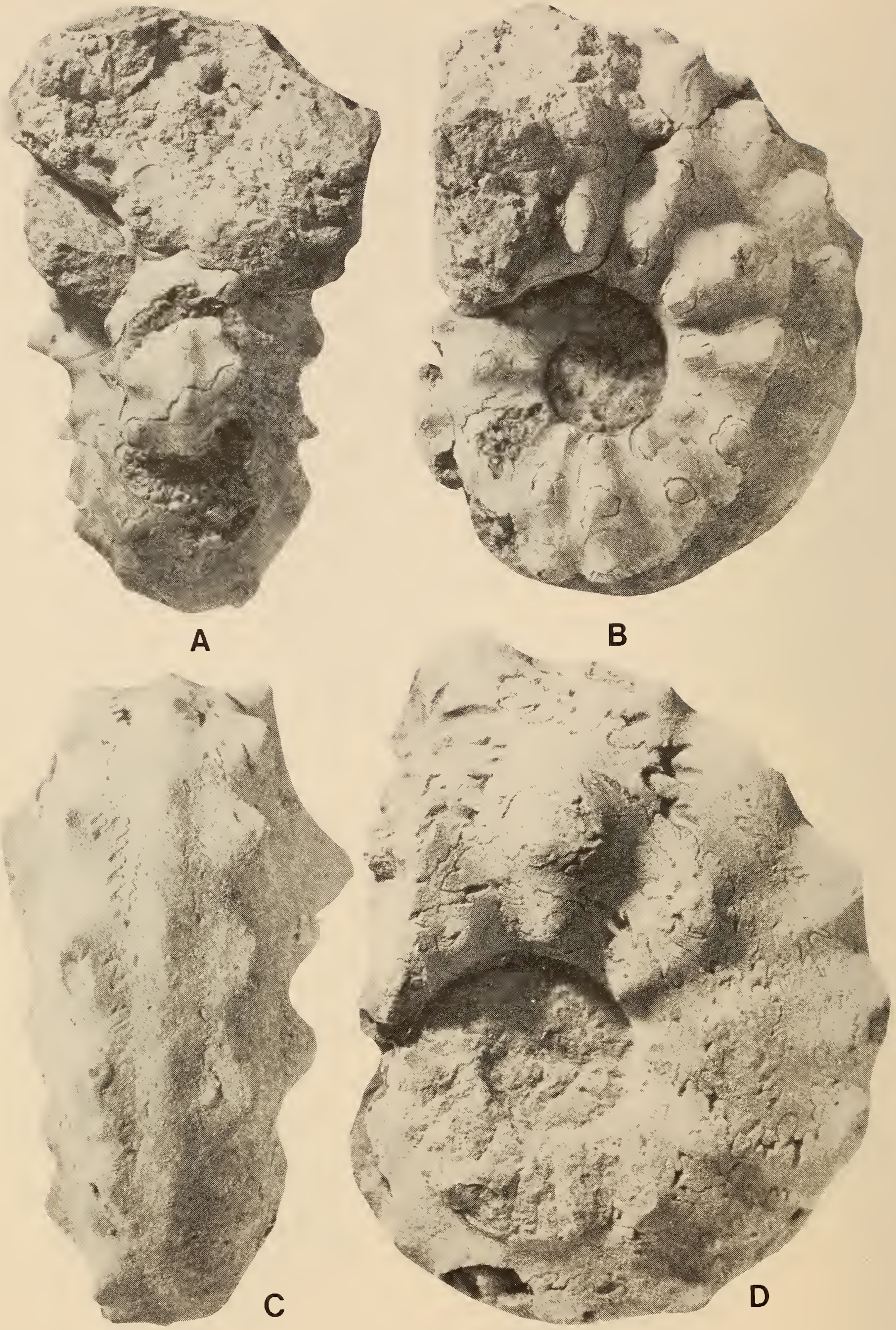

Fig. 25. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A–B. Holotype of '*Collignoniceras peregrinator*' van Hoepen, 1968, SAS Z18. C–D. SAS Z714. All ×1.

Material

SAM–D1187J, from locality 145 at Morrisvale, Zululand, St. Lucia Formation, Coniacian II.

Dimensions

D	*Wb*	*Wh*	*Wb : Wh*	*U*
182,0(100)	—(—)	69,5(38,2)	—	65,0(35,7)

Description

This specimen is a worn internal mould retaining traces of recrystallized shell. Approximately two-thirds of the outer whorl is body chamber.

The coiling is very evolute, the umbilicus comprises 35,7 per cent of the diameter and only 20 per cent of the previous whorl is covered. The umbilicus is shallow, the umbilical wall low and vertical. The whorl section is compressed, with an estimated whorl breadth to height ratio of 0,85–0,90, the greatest breadth being at the lateral tubercle in costal section and close to the umbilical shoulder in intercostal section.

There are seventeen primary ribs on the outer whorl. On the first half, which is the best preserved, the low vertical umbilical wall terminates in an abruptly rounded umbilical shoulder bearing small and variably developed umbilical bullae.

From these arise broad and somewhat weak, straight prorsiradiate ribs that extend to mid-flank, where they bear midlateral tubercles that vary irregularly from weak to massive. These give rise to a pair of straight ribs that connect with small obliquely placed ventrolateral clavi from which low, broad ribs sweep forward in a broad chevron, the apex of which is a strong, elongate siphonal clavus.

Similar ornament is locally preserved on the very worn body chamber, where the irregular development of lateral tubercles is especially noticeable.

Where the inner whorls are visible the ribs seem to be relatively stronger and coarser with respect to the tuberculation than on the outer whorls.

The sutures are too worn for useful description.

Remarks

This specimen has closely similar proportions to, and shows the same style of ribbing and tuberculation as, the unique holotype of *Forresteria (Forresteria) hobsoni* (Reeside) (1932: 18, pl. 9 (figs 2–4), pl. 10 (figs 1–2)) (Fig. 35A–B herein). The latter is more evolute, however, with an outward sloping umbilical wall. To what degree this and other minor differences reflect the different preservations (distorted chalk composite internal mould in *F. (F.) hobsoni*, worn sandstone mould in the African specimen) cannot be ascertained with such limited material, as a result of which the present specimen is identified as *F. (F.)* cf. *hobsoni*. This specimen shows the same style of ornament as the more numerous *F. (F.) madagascariensis* with which it occurs, especially in

Fig. 26. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Holotype of '*Forresteria hammersleyi*' van Hoepen, 1968, SAS Z976. ×1.

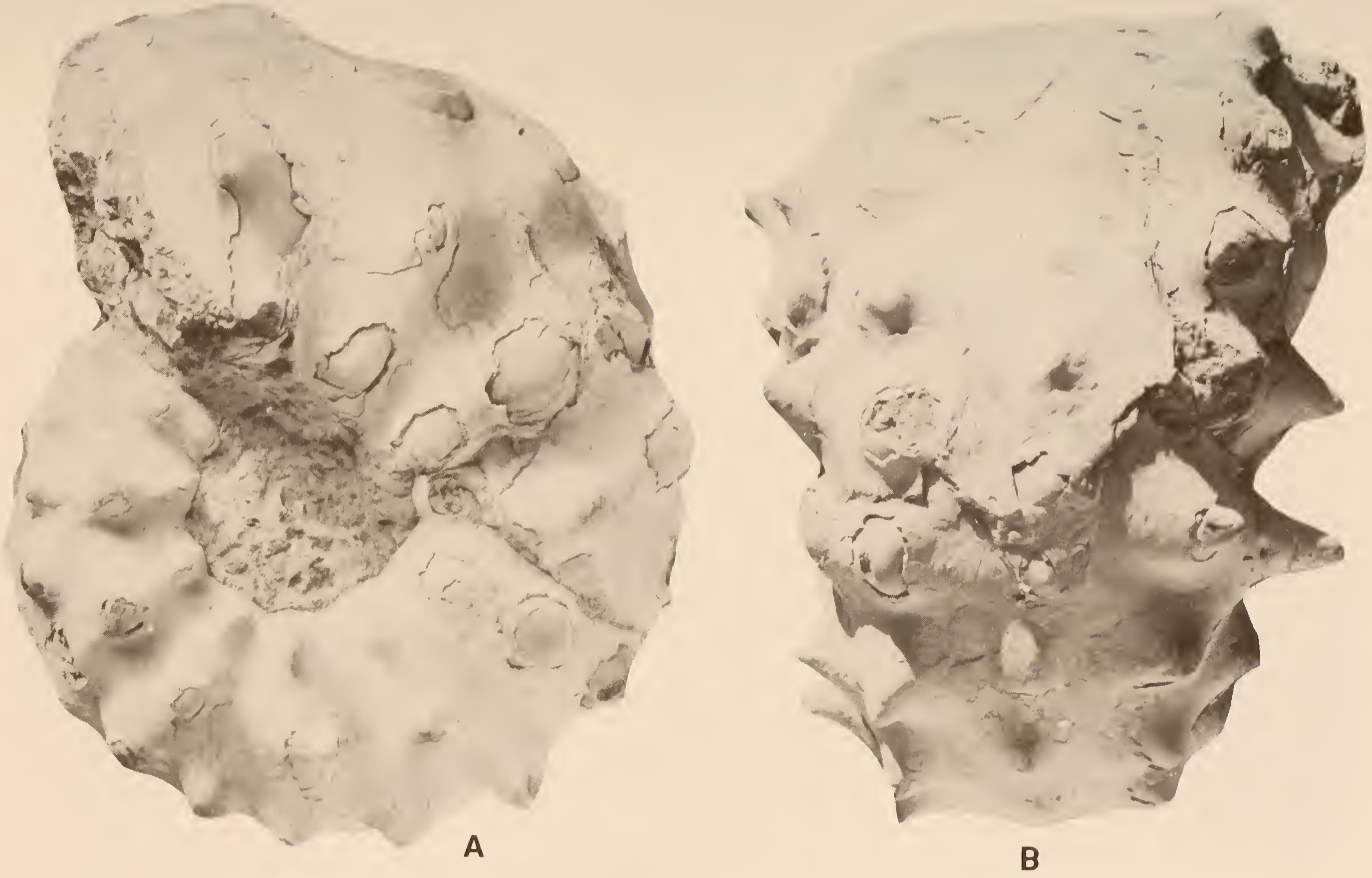

Fig. 27. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). SAS Z969. ×1.

Fig. 28. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Adult ?microconch with body chamber, SAS Z923. ×1.

terms of variable lateral tuberculation and ventrolateral ribbing and tuberculation. It may, indeed, be no more than the compressed and relatively weakly ornamented end of the variation range in the species, but it is not possible to tell on the basis of the available material; if true, the specific name *hobsoni* has priority over *madagascariensis*.

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

Forresteria (Forresteria) madagascariensis (Collignon, 1965)

Figs 10C–D, 15 C–D, 36–38

Neokanabiceras madagascariense Collignon, 1965: 42, pl. 432 (figs 1784–1786, 1787 (var. *ankinatsyensis*)). Wiedmann in Herm, Kauffman & Wiedmann, 1979: 44, pl. 7 (figs A–B); text-fig. 7D.

Neokanabiceras apambiense Collignon, 1965: 44, pl. 432 (fig. 1788).

Holotype

The original of Collignon (1965: 42, pl. 432 (fig. 1784)) from the middle Coniacian Zone of *Kossmaticeras theobaldi* and *Barroisiceras onilahyense* of Ankinatsy (Belo sur Tsiribihina), Madagascar.

Material

SAM–D1187A–I and SAS Z1084A, from 'Pisana', on the Msindusi River, presumably equivalent to locality 145 of Kennedy & Klinger (1975), St. Lucia Formation, Coniacian II.

Dimensions

		D	*Wb*	*Wh*	*Wb*:*Wh*	*U*
SAM–D1187H	*c*	43,2(100)	24,3(56,3)	17,8(41,2)	1,37	12,7(29,4)
	ic		20,5(47,5)	15,8(36,6)	1,30	
SAM–D1187I	*c*	43,9(100)	27,7(63,0)	18,9(43,0)	1,47	11,8(26,9)
SAM–D1187D	*c*	93,0(100)	50,5(54,3)	36,0(38,7)	1,40	32,3(34,7)
	ic		39,3(42,3)	34,2(36,8)	1,15	
at D =	*c*	78,5(100)	46,2(58,9)	30,0(38,2)	1,54	28,3(36,1)
	ic		35,8(45,6)	27,8(35,4)	1,29	
SAM–D1187C	*c*	105,5(100)	—(—)	41,7(39,5)	—	36,1(34,2)
		128,0(100)	68,8(53,8)	50,0(39,0)	1,38	41,2(32,2)
			54,5(42,6)	46,8(36,6)	1,16	

Description

All the available specimens are internal moulds retaining traces of shell. The largest, SAM–D1187A, is still septate at a diameter of 130 mm.

The earliest visible stages are shown by SAM–D1187I (Fig. 10C–D). The coiling is evolute, with a deep umbilicus (26–34% of diameter). The whorl section is depressed, coronate (whorl breadth to height ratio is 1,3 to 1,4 in intercostal, and 1,37 to 1,47 in costal section) the maximum breadth at the massive lateral tubercles in costal section and low on the flank in intercostal

Fig. 29. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). SAS Z979. ×1.

Fig. 30. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A pathological body chamber, SAS Z977. ×1.

Fig. 31. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Holotype of '*Forresteria itwebae*' van Hoepen, 1968, SAS Z250. ×1.

section. Twelve or thirteen strong, broad, rounded ribs arise at the umbilical seam. They develop umbilical bullae of variable strength and pass slightly prorsiradiate across the flanks to massive conical mid-lateral tubercles. These give rise to a pair of straight or feebly concave ribs that link to strong oblique ventral clavi twice as numerous as the lateral tubercles. These in turn give rise to weaker, broad prorsiradiate ribs that form a chevron over the venter with a strong siphonal clavus at the apex of the 'V'.

Even at this diameter there is great variation in the relative strengths of tubercles and ribs, the former dominating in SAM–D1187G, the latter in SAM–D1187I.

Two slightly larger fragments, SAM–D1187E and F, show essentially similar ornament at estimated diameters of 70 mm; SAM–D1187E (Fig. 36A–B) shows the beginning of differentiation in strength of the lateral tubercles, every fourth one of which is much stronger than the others, while SAM–D1187F has shell preserved on sharp, high siphonal clavi (Fig. 15C–D).

SAM–D1187D shows the ornamentation at a diameter of 93 mm. There are twelve to thirteen strong ribs per whorl, bearing weak to strong umbilical bullae that link to variable strong to massive lateral tubercles. These give rise to pairs of strong ribs linking to strong ventral clavi from which weaker, broad ribs form a chevron linking to the strong, sharp siphonal clavi.

SAM–D1187D (Fig. 36C–D) is a comparable specimen with approximately 110 mm diameter. The style of ornament on the first half of the outer whorl is similar, if less hypernodose, while on the outer whorl ribbing is relatively better developed with respect to the tubercles. Both these specimens and SAM–D1187B, a rather poorly preserved individual, also show occasional primary ribs without umbilical bullae or lateral tubercles. The largest specimen, SAM–D1187A (Fig. 37A–B), maintains the same style of ornament described above, with thirteen strong, tuberculate primary ribs per whorl.

The suture line is incompletely exposed on SAM–D1187C only. E/L is elongate, rectangular, little incised, and asymmetrically bifid, L is narrow and deep.

Discussion

The specimens referred to this species vary greatly in proportions and relative development of ribs and tubercles, but are linked by coronate form, sparse primary ribs, massive, if variable lateral tubercles, paired outer flank ribs, and ventral and siphonal clavi. They match closely with the types of *Neokanabiceras madagascariense* Collignon (1965: 42, pl. 432 (figs 1784–1786)) and encompass the predominantly ribbed var. *ankinatsyensis* Collignon (1965: 43, pl. 432 (fig. 1878)). The authors have little doubt that, given a somewhat larger collection, *Neokanabiceras apambiense* Collignon (1965: 43, pl. 432 (fig. 1788)) would prove to be no more than a very depressed variant of this species.

Fig. 32. *Forresteria (Forresteria)* cf. *hobsoni* (Reeside, 1932). SAM–D1187. ×0,78.

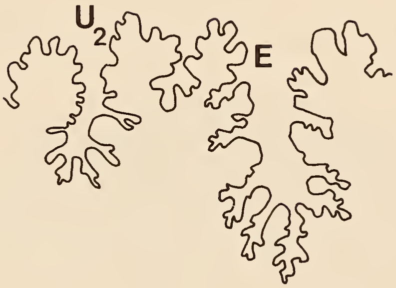

Fig. 33. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). External suture of an inflated specimen, SAS Z1438. ×2.

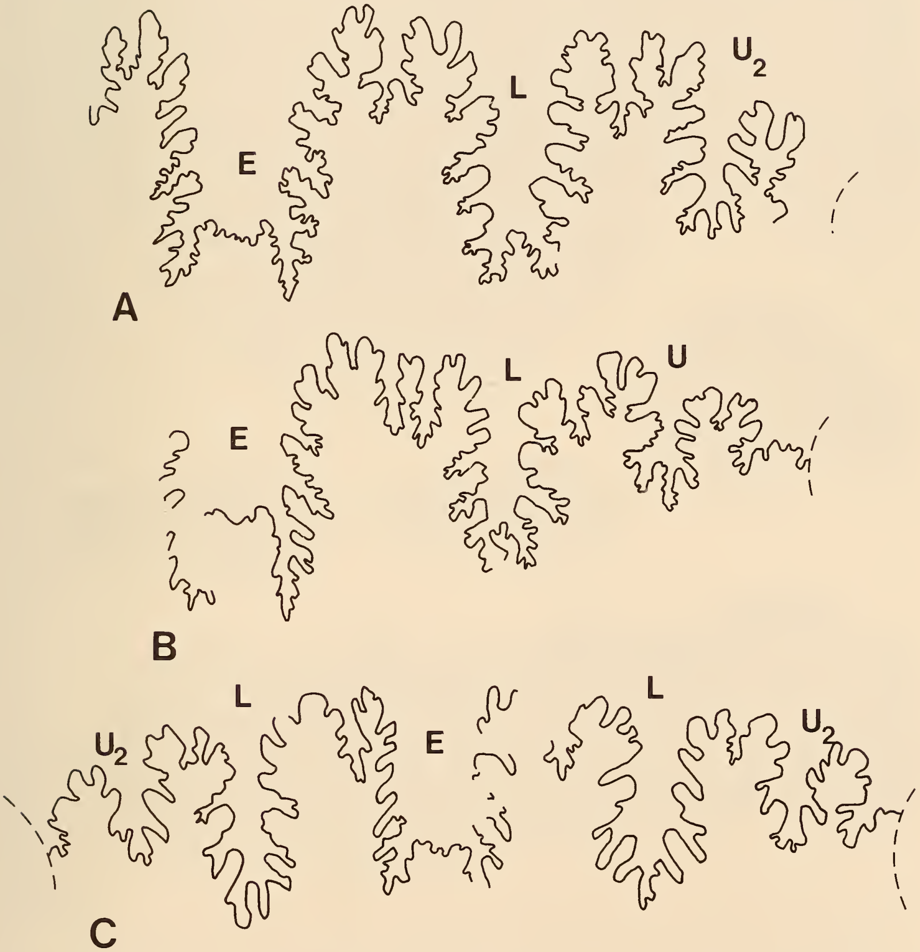

Fig. 34. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Showing external sutures. A. A compressed specimen, SAS Z1429. B. A compressed specimen, SAS Z978. C. A pathological specimen, SAS Z1523. All ×2.

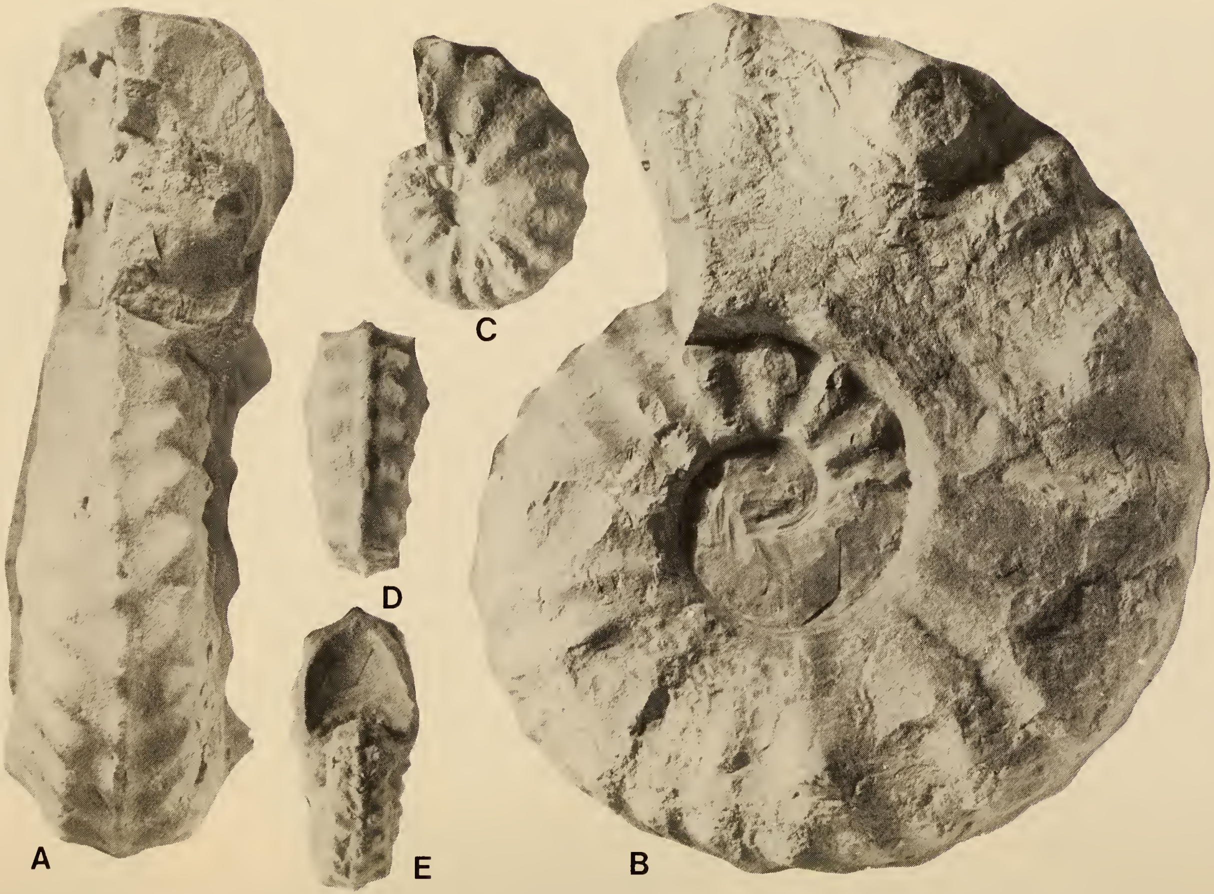

Fig. 35. A–B. *Forresteria (Forresteria) hobsoni* (Reeside, 1932). The holotype from the Timpas Limestone near Carlile Springs, Colorado, USNM 73762. ×0,67. C–E. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). A paratype of '*Barroisiceras (Forresteria) stantoni*' Reeside (1932, pl. 7 (figs 3–7)). ×1.

There is close resemblance to *Forresteria (Forresteria) hobsoni* Reeside (1932: 18, pl. 9 (figs 2–4), pl. 10 (figs 1–2)), a species originally described from the Coniacian of the United States Western Interior and refigured here as Figure 35A–B. A single specimen compared with this species occurs with the collection of *F. (F.) madagascariensis*, but differs in being compressed rather than depressed and with more primary ribs per whorl. It does, however, show a similar strong and variably developed lateral tubercle that gives rise to pairs of ribs linking to ventral clavi that in turn link to a ventral chevron and row of siphonal clavi. This specimen may be simply a compressed variant of a population that encompasses both *F. (F.) madagascariensis* and *F. (F.) hobsoni* (the latter name having priority), but as the type of *F. (F.) hobsoni* is the only known specimen from the United States, this cannot be certain, and they are maintained separate.

There are also similarities to *Yabeiceras transiens* sp. nov. (Fig. 46A–C), described and discussed below, which points to the close affinities of *Yabeiceras* and *Forresteria*.

When compared to the variable *Forresteria (Forresteria) alluaudi* described above, the most obvious differences are to be found in the combination of massive lateral tubercles and strong ribs, plus the presence of a ridge supporting the siphonal clavi.

There is a closer similarity to *Forresteria (Forresteria) nwalii* (Reyment, 1976) (in Offodile & Reyment 1976: 61, fig. 14A–B), the holotype of which is re-illustrated here as Figure 39A–B. There are a similar number of strong primary ribs in both species with a weaker umbilical than lateral tubercle, the latter variably and massively developed. In *F. (F.) nwalii*, however, it is pinched and narrow, the pairs of ribs linking to the ventral clavi are stronger and not uncommonly accompanied by one or two weaker additional ribs looping between lateral and ventral tubercles. In the Nigerian form, which has an altogether clumsier ornament, the ventral clavi are relatively larger, ventral ribs stronger, and chevron angle larger.

Occurrence

St. Lucia Formation, Coniacian II, of Zululand; Coniacian of Madagascar.

Genus *Yabeiceras* Tokunaga & Shimizu, 1926
(= *Eboroceras* Basse, 1946)

Type species

Yabeiceras orientale Tokunaga & Shimizu (1926: 20, pl. 22 (fig. 7), pl. 27 (fig. 1)) from the Coniacian of Japan, by the original designation of Tokunaga and Shimizu (1926: 20).

Diagnosis

Very evolute. Inner whorls depressed, coronate, with lateral tubercles, oblique ventrolateral tubercles twice as numerous as the lateral, and a rounded siphonal ridge with low clavi. These persist into middle growth in some species. In others the tubercles decline and are replaced by ribs; the venter has a rounded siphonal ridge flanked by variably developed grooves, the outer edges of which may be slightly raised. Ornament persists in some species, in others the outer whorl is smooth or has a ventral keel and sulci only. Smooth body chambers develop at disparate sizes, suggesting a size dimorphism.

Suture with rather narrow, deeply incised elements.

Discussion

The inner whorls of *Yabeiceras* are so similar to those of *Forresteria (Forresteria)* that close affinity cannot be doubted; it is a member of the subfamily Barroisiceratinae (compare Figs 11A–K, 41A–D) as Matsumoto *et al.* (1964) and Matsumoto (1969) have shown. *Yabeiceras transiens* sp. nov., described below (p. 303), shows an intermediate morphology even in middle growth (Fig. 46). *Forresteria (Harleites)* appears at the base of the Coniacian (Hancock & Kennedy 1981; Kennedy, Wright & Hancock 1982) and the line of descent is taken here to be *F. (Harleites)* → *F. (Forresteria)* → *Yabeiceras*.

Eboroceras Basse (1946: 73), type species *Eboroceras magnumbilicatum* Basse (1946: 73, pl. 2 (fig. 2), text-fig. 2), is a clear synonym. *Yabeiceras* is a very rare genus in terms of numbers and, as is commonly the case, many species have been described that differ only in details:

1. *Yabeiceras orientale* Tokunaga & Shimizu, 1926: 20, pl. 22 (fig. 7). Shimizu, 1926: 547. Matsumoto *et al.* 1964: 323, pl. 48 (figs 1–2), text-figs 1–3. Matsumoto, 1969: 324, pl. 44 (figs 1–2), pl. 45 (fig. 1), text-figs 12–13. The unique holotype from the upper reaches of the Sakurazawa in Oriki, Japan, was destroyed in World War II. Two specimens are known from the Futaba area of north-eastern Japan (Matsumoto *et al.* 1964) and two more are described by Matsumoto (1969).

2. *Yabeiceras kotoi* Tokunaga & Shimizu, 1926: 202, pl. 22 (fig. 8), pl. 28 (fig. 16). This was based on a single specimen from the same horizon and locality as the holotype of *Y. orientale*, and was also destroyed by fire.

3. *Yabeiceras himuroi* Tokunaga & Shimizu, 1926: 203, pl. 22 (fig. 9), pl. 27 (fig. 2). This was based on a single fragment with the same origin and fate as the previous species. It is best treated as a *nomen dubium*.

4. *Yabeiceras magnumbilicatum* (Basse, 1946): Basse, 1946: 73, pl. 2, (fig. 2), text-fig. 2. Collignon, 1965: 82, pl. 451 (fig. 1835): 84, pl. 452 (fig. 1837). This species was described on the basis of the holotype only. Two other specimens are described by Collignon. All are from Madagascar.

5. *Yabeiceras bituberculatum* Collignon, 1965: 82, pl. 451 (fig. 1836): 84, pl. 452 (fig. 1838). Two specimens only have been illustrated, from the *Kossmaticeras theobaldi* and *Barroisiceras onilahyense* Zone of Ampozaloaka, Madagascar.

6. *Yabeiceras manasoaense* Collignon, 1965: 84, pl. 452 (fig. 1839). Matsumoto, 1971: 144, pl. 24 (fig. 2), text-fig. 9. Klinger *et al.*, 1976: 162, figs 1–4. The holotype is from the same horizon as the previous species at Manasoa (Betioky), Madagascar. Two others, from Japan and the South African offshore Alphard Group, have also been described.

7. *Yabeiceras menabense* Collignon, 1965: 86, pl. 453 (fig. 1840). The holotype is the only described specimen and is from the *Peroniceras dravidicum* Zone of Ankinatsy-Souroumaraina (Belo sur Tsiribihina), Madagascar.

8. *Yabeiceras costatum* Collignon, 1965: 87, pl. 454 (fig. 1841). The holotype is the only described specimen and is from the same horizon and locality as the previous species.

9. *Yabeiceras ankinatsyense* Collignon, 1965: 87, pl. 454 (fig. 1842). Only the holotype was described and is from the same horizon and locality as the previous species.

It will be seen that there are only 17 described specimens of *Yabeiceras*, 8 from Japan, referred to 4 species, 8 from Madagascar, referred to 5 species, and 1 from the South African offshore Alphard Group.

The present collection of fourteen specimens from Zululand nearly doubles the described material of this genus. Unfortunately it complicates rather than clarifies the taxonomy; because there are so few specimens, the authors cannot assess the limits of intraspecific variability nor gauge the effect of suspected yet unconfirmed dimorphism. In contrast to the genus *Forresteria*, where the extent of intraspecific variation could satisfactorily be demonstrated, a conservative morphological taxonomy is therefore followed below, with many species that may prove to be no more than fragments of one or a few variable species.

Occurrence

Coniacian of Japan, Madagascar, Zululand, and the South African offshore Alphard Group.

Yabeiceras orientale Tokunaga & Shimizu, 1926

Figs 41, 42G–I, 45

Yabeiceras orientale Tokunaga & Shimizu, 1926: 20, pl. 22 (fig. 7), pl. 27 (fig. 1). Shimizu, 1926: 547. Matsumoto *et al.*, 1964: 323, pl. 48 (figs 1–2), text-figs 1a–d, 2a–e, 3. Matsumoto 1969: 324, pl. 44 (figs 1–2), pl. 45 (fig. 1), text-figs 12–13.

Holotype

The original of Tokunaga & Shimizu (1926: 20, pl. 22 (fig. 7), pl. 27 (fig. 1a–c)), from the Coniacian Futaba Formation of the upper reaches of the Sakurazawa in the Oriki, north-eastern Japan, destroyed in World War II.

Material

SAS H196/1, from the west bank of the Hluhluwe River, Zululand, 32°19′30″E 28°5′30″S, St. Lucia Formation, Coniacian II.

Fig. 36. *Forresteria (Forresteria) madagascariensis* (Collignon, 1965). A–B. SAM–D1187E. C–D. SAM–D1187D. All ×1.

Fig. 37. *Forresteria (Forresteria) madagascariensis* (Collignon 1965). SAM–D1187A. ×1.

Fig. 38. *Forresteria (Forresteria) madagascariensis* (Collignon, 1965) SAM-D1187C. ×1.

Dimensions

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
c	64,0(100)	26,5(41,4)	18,5(28,9)	1,43	29,3(45,8)
ic	64,0(100)	23,8(37,2)	18,5(28,9)	1,29	29,3(45,8)

Description

The earliest stage visible is at a diameter of 20 mm (Fig. 41C–D). The coiling is evolute with a deep umbilicus, the whorl section depressed, with the greatest breadth low on the flank intercostally and at the lateral tubercle costally. There are thirteen to fourteen strong primary ribs per whorl, arising on the umbilical shoulder. They develop into strong bullate to conical umbilicolateral tubercles that increase rapidly in strength as size increases. At the smallest diameter visible these tubercles give rise to pairs of strong prorsiradiate ribs that terminate in oblique ventral clavi. A shallow depression separates these from a corresponding number of siphonal clavi. This same style of ornament continues to 20 mm but the ribs become broader and lower. Beyond this the whorl section becomes very depressed, the tubercles conical and progressively stronger to a diameter of about 50 mm, at the same time migrating outwards from the umbilicus (Fig. 42G–I). The ribs progressively decline and are effaced on the outer flank, the ventral grooves are weak, and a line of low, weak siphonal clavi is still visible.

The coiling is very evolute on the outer whorl, less than 25 per cent of the previous whorl being covered. The whorl section is depressed and reniform, with an intercostal whorl breadth to height ratio of 1,29 and a costal ratio of 1,43, the greatest breadth being close to the umbilical shoulder.

The flanks are reduced and the venter is very broad and rounded. The umbilicus is of moderate width, comprising 45 per cent of the diameter, with a low, rounded, outward-sloping wall indented to accommodate the tubercles of the preceding whorl.

Ornament consists of eighteen strong, broad primary ribs arising at the umbilical wall and developing into strong umbilicolateral tubercles. These are initially conical but become progressively bullate as size increases. Single ribs or pairs of low, rounded, concave, prorsiradiate ribs arise from these tubercles, sweep forward over the ventrolateral shoulders and become increasingly weakened as size increases, terminating in weak, obliquely placed ventral clavi. These are separated by a feeble, broad groove from a spiral siphonal swelling that bears low, rounded clavi corresponding to the ventrolaterals.

The suture line is well exposed (Fig. 45).

Discussion

This interesting specimen shows the ontogenetic development from a diameter similar to that of specimens of *Yabeiceras orientale* described by Matsumoto *et al.* (1964), to which it is essentially identical. The change in tuberculation round the outer whorl is comparable to that in *Y. orientale*,

Fig. 39. *Forresteria (Forresteria) nwalii* (Reyment, 1976). The holotype from Nkalagu, Anambra State, Nigeria. ×1.

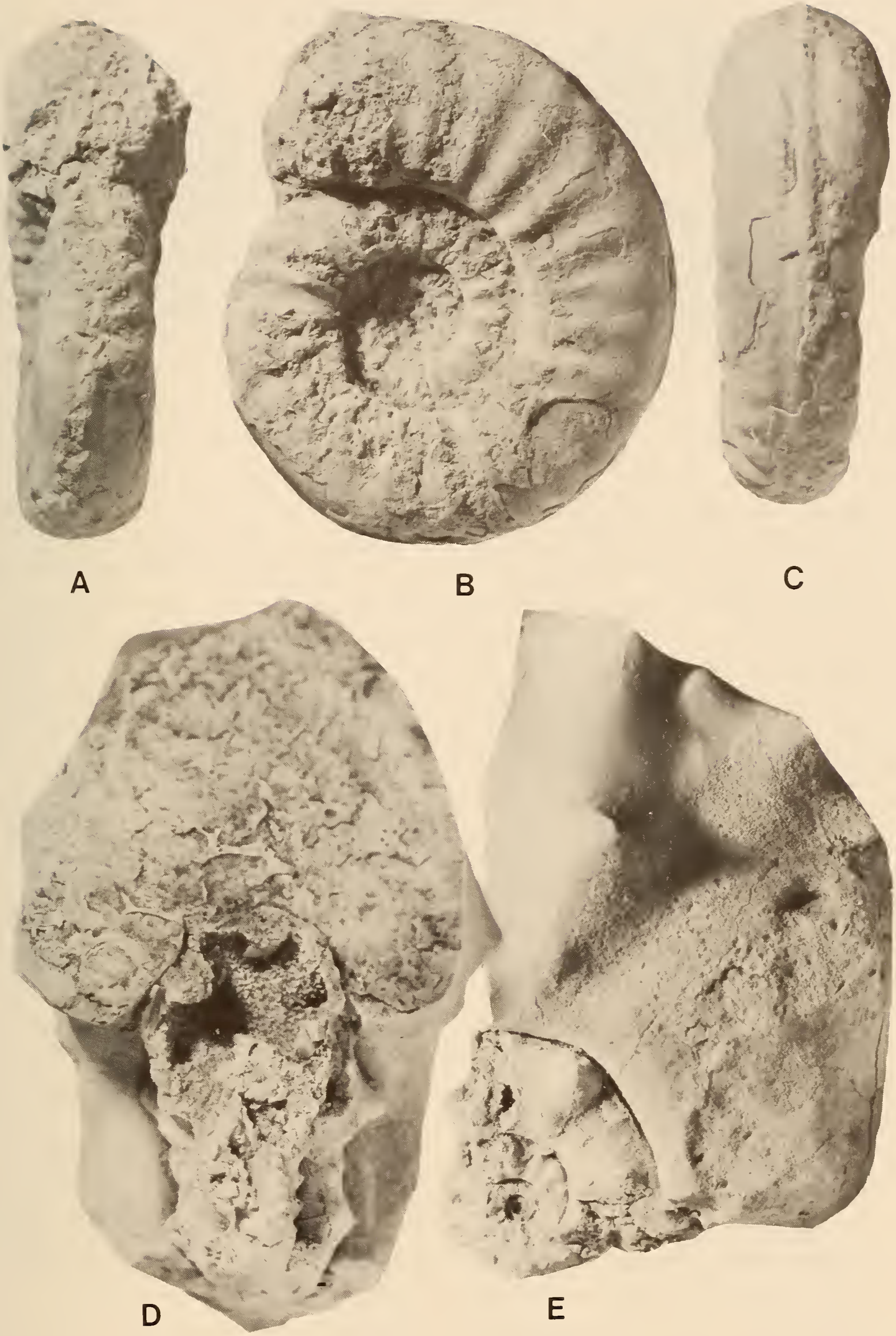

Fig. 40. A–C. *Yabeiceras costatum* Collignon, 1965. SAM–D1188C. D–E. *Forresteria (Forresteria) alluaudi* (Boule, Lemoine & Thévenin, 1907). Inner whorls of the holotype of '*Forresteria itwebae*' van Hoepen, 1968, SAS Z250. All ×1.

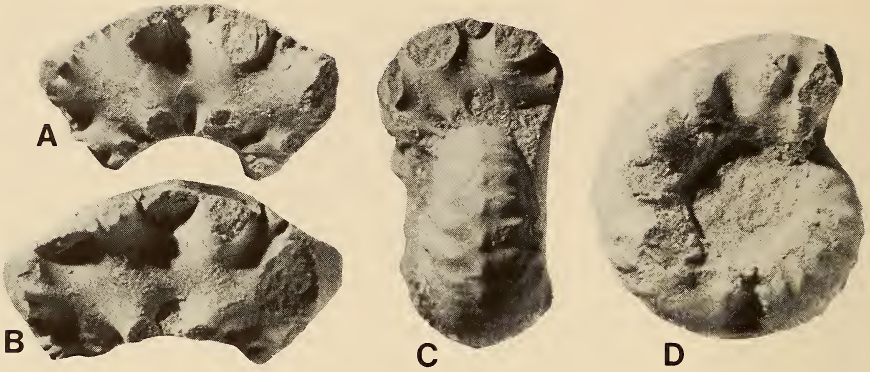

Fig. 41. *Yabeiceras orientale* Tokunaga & Shimizu, 1926. Inner whorls of SAS H196/1. ×2.

although occurring at a slightly different diameter. It is too small to show the change from depressed tuberculate whorls to high, compressed, smooth whorls of adult *Y. orientale* (e.g. Figs 43–44), but in spite of this the authors believe it to represent the same species.

Occurrence

The species is known from the Futaba area of north-eastern Japan and from Hokkaido. The present specimen is from the St. Lucia Formation, Coniacian II, of Zululand.

Yabeiceras cf. *orientale* Tokunaga & Shimizu, 1926

Fig. 42A–C

Compare

Yabeiceras orientale Tokunaga & Shimizu, 1926: 20, pl. 22 (fig. 7), pl. 27 (fig. 1).

Material

SAM–D1188F, from locality 145 in the Morrisvale area to the north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Discussion

This poorly preserved juvenile has sixteen primary ribs with rather strong umbilicolateral tubercles. It most closely recalls *Y. orientale*, discussed above.

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

Yabeiceras transiens sp. nov.

Fig. 46

Holotype

SAM–D1188A, by monotypy, from locality 145 in the Morrisvale area to the north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Etymology

Refers to the transitional features of the species between *Forresteria* and *Yabeiceras*.

Dimensions

c	83,9(100)	40,5(48,3)	32,0(38,1)	1,27	30.3(36,1)
ic		35,0(41,7)	31,8(37,9)	1,1	
	68,5(100)	32,9(48,0)	25,4(37,1)	1,30	24,4(35,6)
		29,5(43,1)	25,0(36,5)	1,18	

Description

The holotype and only known specimen is a well-preserved, wholly septate mould retaining traces of recrystallized shell. Coiling is moderately evolute with approximately 40 per cent of the previous whorl being covered. The whorl section is depressed; at the beginning of the outermost whorl the whorl breadth to height ratio is 1,65, the costal section polygonal, and the intercostal section a depressed oval. At the greatest preserved diameter the whorl breadth to height ratio is 1,27 costally and 1,1 intercostally, the greatest breadth being at the lateral tubercle on the ribs and close to the umbilical shoulder intercostally. The umbilicus comprises 36,1 per cent of the diameter, is relatively deep with a flattened, vertical umbilical wall and abruptly rounded umbilical shoulder. There are eighteen primary ribs on the outer whorl. These bear well-developed umbilical bullae of variable strength. They are prorsiradiate and straight or slightly concave, strong and bar-like to mid-flank where they bear a lateral tubercle. This is strong and spinate at the smallest diameter visible but declines around the outer whorl, becoming bullate. Each lateral tubercle gives rise to a pair of somewhat weaker, broader, rounded ribs that bear strong, obliquely placed ventrolateral clavi, an estimated total of thirty to thirty-three per whorl. These project forward over the venter where they are interrupted by a broad shallow groove on either side of a rounded siphonal keel. This bears distinct siphonal clavi at the smallest diameter visible, corresponding in number to, but displaced adaperturally of, the ventrolateral clavi. These decline around the outer whorl giving a low, undulose keel at the greatest diameter preserved.

The suture line is incompletely exposed. E/L is broad and bifid with moderate incision; L deep, narrow and bifid; L/U_2 smaller and symmetrically bifid.

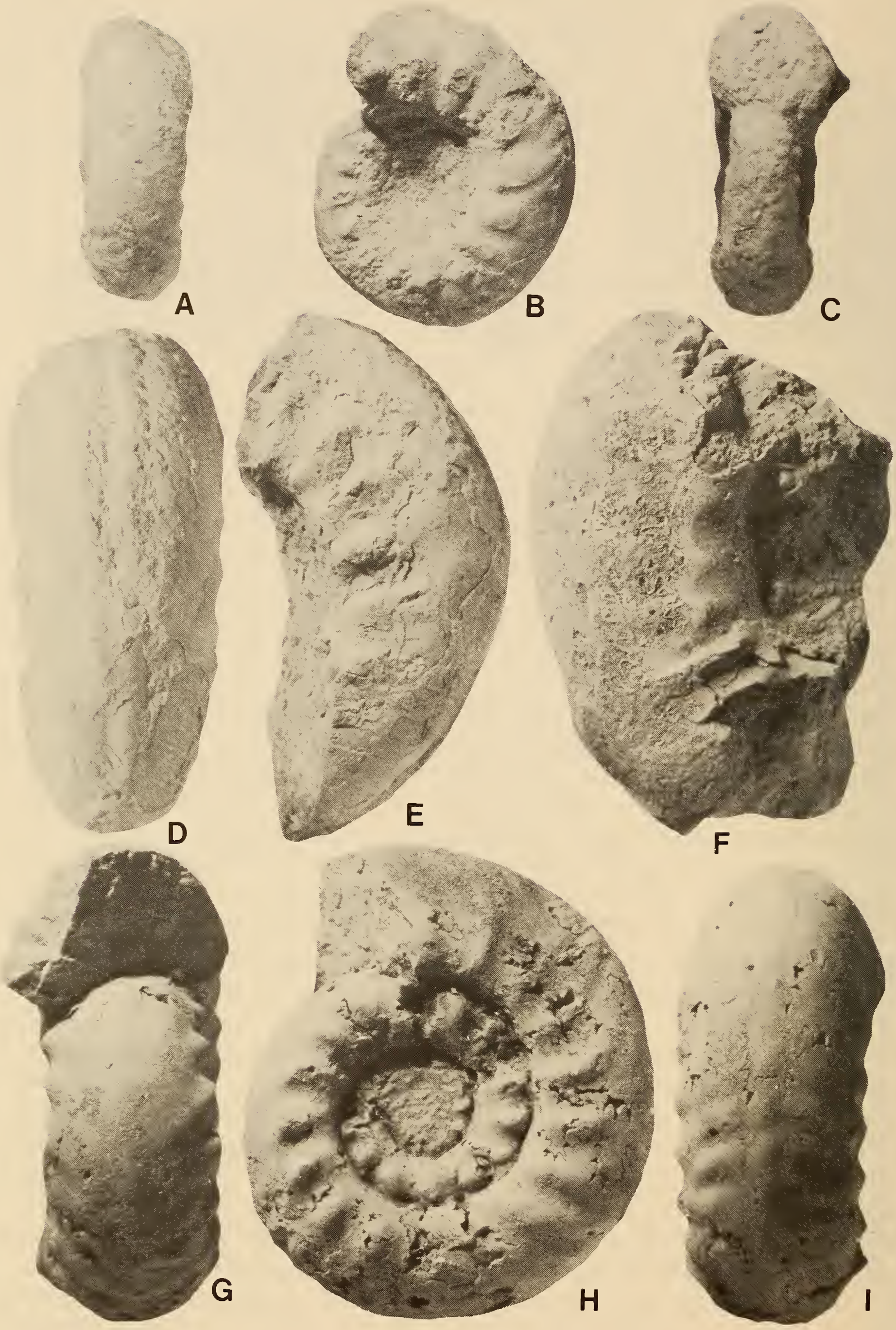

Fig. 42. A–C. *Yabeiceras* cf. *orientale* Tokunaga & Shimizu, 1926, SAM–D1188F. D–E. *Yabeiceras costatum* Collignon, 1965, SAM–D1188E. F. *Yabeiceras* sp. indet., SAM– D1182. G–I. *Yabeiceras orientale* Tokunaga & Shimizu, 1926, SAS H196/1. All ×1.

Fig. 43. *Yabeiceras orientale* Tokunaga & Shimizu, 1926. From the upper reaches of the Ikushumbets, Hokkaido, Japan, Kyūshū University Collections H5624. ×1.

Discussion

As suggested by the name, this new species combines features of both *Yabeiceras* and *Forresteria*, having inner whorls with strong ribs and tubercles like the latter and a carinate-bisulcate venter like *Yabeiceras* that retains traces of siphonal clavi to a much greater diameter than any other species referred to the genus.

The only described species with which it is likely to be confused is *Yabeiceras bituberculatum* Collignon (1965: 82, pl. 341 (fig. 1836), pl. 342 (fig. 1838)). They differ in that the ribs are relatively stronger and more numerous in the new species and bear umbilical bullae throughout, while ribbing and tuberculation are retained to a diameter where *Y. bituberculatum* has already developed a smooth, constricted body chamber. Among *Forresteria (Forresteria)* species, the closest resemblance is to *F. (F.) madagascariensis* with which it occurs (see above). All the specimens of this species are stronger ribbed with massive, variable lateral tubercles, stronger ventrolateral and siphonal clavi and no obvious ventral sulci. In the *F. (Forresteria)*-like inner and smoothing outer

Fig. 44. *Yabeiceras orientale* Tokunaga & Shimizu, 1926. Tohuko University Collections IGPS 35342, from the Bibai, Ishikari Province, Hokkaido, Japan. ×1.

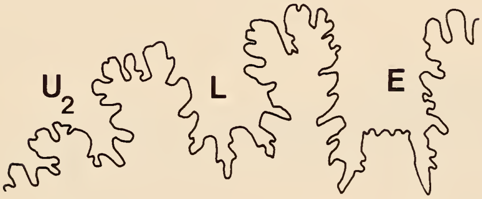

Fig. 45. *Yabeiceras orientale* Tokunaga & Shimizu, 1926. External suture of SAS H196/1. ×2.

whorls there is a resemblance to *F. (Muramotoa)*, but all described species are more involute and high-whorled and show a rapid loss of ornament.

It may be that *Yabeiceras transiens* is a micromorph and perhaps a microconch of some other barroisiceratid, for, as has been noted above, both micro- and macromorph taxa occur throughout the family (see p. 242).

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

Yabeiceras ankinatsyense Collignon, 1965

Fig. 50C–D

Yabeiceras ankinatsyense Collignon, 1965: 87, pl. 454 (fig. 1842).

Holotype

The original of Collignon (1965: 87, pl. 454 (fig. 1842)), from the *Peroniceras dravidicum* Zone of Ankinatsy (Belo sur Tsiribihina), Madagascar.

Material

SAS H196/3, from the west bank of the Hluhluwe River, 32°19′30″E 28°5′30″S Zululand, St. Lucia Formation, Coniacian II.

Dimensions

	D	*Wb*	*Wh*	*Wb : Wh*	*U*
SAS H196/3	34,2(100)	15,5(45,3)	12,8(37,4)	1,2	8,2(24,0)
Holotype (after Collignon)	70,0(100)	24,0(34)	24,0(34)	1,0	27,0(39)

Description

This specimen is only 34,2 mm in diameter, moderately evolute with a rather small umbilicus comprising 24 per cent of the diameter. The whorl section is a depressed oval in intercostal section, with the greatest width low on the flanks and at the umbilical bullae in costal section. The umbilical wall is subvertical, undercut, and of moderate elevation, the umbilical shoulder abruptly rounded, the inner flanks moderately inflated, the outer flattened, with a broadly rounded, flattened venter.

Fig. 46. *Yabeiceras transiens* sp. nov. Holotype, SAM-D1188A. ×1.

There are sixteen strong, narrow ribs per whorl. These arise as mere striae at the umbilical seam but strengthen at the umbilical shoulder, developing feebly defined bullae. They are strong, rounded and narrow on the inner half of the flanks, straight and prorsiradiate, and bear a strong, sharp, bullate lateral tubercle. The lateral tubercles usually give rise to pairs of weak, concave secondaries that are accompanied by a few intercalated secondaries to give a total of thirty ribs per whorl on the outer parts of the flanks. These sweep forward across the ventrolateral shoulder where they terminate in low, swollen, oblique ventrolateral clavi. There is a low, broad, rounded undulose siphonal ridge flanked by shallow grooves, developing ill-defined siphonal clavi corresponding in position and number to the ventrolateral clavi.

The sutures are not exposed.

Discussion

Few *Yabeiceras* species are known at this diameter but all those that are show the umbilicolateral, ventrolateral, and siphonal tuberculation of the present specimen to various degrees. *Y. orientale* Tokunaga & Shimizu is more depressed with strong lateral tubercles. Strength of tubercles also distinguishes *Y. magnumbilicatum*, *manasoaense*, *menabense*, *transiens*, and *bituberculatum* at this size as far as can be seen from the inner whorls of the much larger type specimens, while there are also differences in number of ribs. The costal whorl sections of *Y. bituberculatum* and *Y. transiens* are markedly polygonal and easily distinguished. The inner whorls of the holotype of *Y. costatum* are much more coarsely and closely ribbed with stronger flank tubercles. The inner whorls of *Y. ankinatsyense* thus provide the closest comparisons—rib density and strength are similar, as far as is visible—but the umbilicus at the admittedly greater diameter (70 compared to 34,5 mm) is much wider (39% compared to 24%) and the whorls are as wide as high rather than depressed. These differences may well be entirely due to the disparate sizes of our specimen and the holotype.

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

Yabeiceras costatum Collignon, 1965

Figs 40A–C, 42D–E

Yabeiceras costatum Collignon, 1965: 87, pl. 454 (fig. 1841).

Material

SAM–D1180C and E, both from locality 145 in the Morrisvale area north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Dimensions

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
SAM–D1188C	68,0(100)	25,5(37,5)	21,5(31,6)	1,19	29,2(43,0)
Holotype (after Collignon 1965)	74,0(100)	29,0(39)	24,0(32)	1,20	36,0(49,0)

Description

SAM–D1180C is a well-preserved specimen, largely septate, and retaining recrystallized shell. The coiling is very evolute, with a broad umbilicus comprising 43 per cent of the diameter. The umbilical wall is relatively low, rounded, and undercut. The whorl section is depressed (whorl breadth to height ratio is 1,19) with the greatest breadth at the lateral tubercles, where present, or at mid-flank. The flanks are flattened and converge to a broadly rounded venter.

There are twenty-five to twenty-six primary ribs per whorl. These arise at the umbilical seam, pass backward across the umbilical wall and strengthen into an umbilical bulla of variable, generally weak development at the umbilical shoulder. The ribs are straight, broad, rounded, and prorsiradiate, strengthen across the inner flank and bear a well-defined pointed midlateral tubercle up to a diameter of 45 mm, beyond which it progressively declines. The ribs weaken across the outer flank; on the first half of the outer whorl, to a diameter of around 55 m, they strengthen as they sweep slightly forward across the ventrolateral shoulder, giving the appearance of an ill-defined oblique, rounded ventral clavus that terminates against a shallow, broad ventral groove flanking the siphonal keel. Beyond 55 mm diameter the ribs weaken markedly over the ventrolateral shoulder.

The siphonal keel is rounded, obscurely undulose at the smallest diameter visible, becoming continuous over the last half whorl.

SAM–D1188E, a partially septate specimen with an estimated original diameter of 75 mm, shows the continuing disappearance of the midlateral tubercle and weakening of the ribs over the ventrolateral shoulder.

The sutures are not exposed.

Discussion

Style of ornament, in particular the predominance of ribbing and early decline of the midlateral tubercle, link this specimen with the holotype of *Y. costatum* Collignon (1965: 87, pl. 454 (fig. 1841)); it differs only in having a slightly narrower umbilicus (43 % compared to 49).

Y. costatum most closely resembles *Y. ankinatsyense* Collignon (1965: 87, pl. 354 (fig. 1842)) from the same horizon at Ankinatsy (Belo sur Tsiribihina), which has slightly different proportions (D = 70 (100); Wb = 24(34,0); Wh = 24(34); U = 27(39,0)), in particular a whorl section as wide as high and a narrower umbilicus (39 % of diameter). There are few ribs—fifteen to sixteen per whorl, concave and, according to Collignon, lacking tubercles. The holotype is the only known specimen.

Y. menabense Collignon (1965: 86, pl. 453 (fig. 1840)) and *Y. manasoaense* Collignon (1965: 84, pl. 452 (fig. 1839)) are easily distinguished by their massive whorls and the development of large umbilicolateral tubercles at diameters comparable to our specimens.

The holotype of *Y. bituberculatum* Collignon (1965: 82, pl. 451 (fig. 136a–c)) again has massive umbilical tubercles; the smaller paratype referred to the species (Collignon 1965: 84, pl. 452 (fig. 1836)) has a polygonal whorl, with massive lateral and prominent ventral tubercles, the latter twice as numerous as the former.

Y. magnumbilicatum (Basse) (1946: 73, pl. 2 (fig. 2a–b) text-fig. 2) has strong, sparse umbilical and lateral tubercles, and loses all ornament on the body chamber.

Of *Yabeiceras* described from Japan, *Y. orientale* Tokunaga & Shimizu, 1926, has fewer, stronger lateral tubercles that give rise to pairs of secondaries with ventral clavi in middle growth and a smooth body chamber.

Y. kotoi Tokunaga and Shimizu (1926: 302, pl. 22 (fig. 8), pl. 26 (fig. 15)), the types of which were destroyed in World War II, has not been discussed by subsequent Japanese workers. According to the original account it is compressed (whorl breadth to height ratio is 0,83 at a diameter of 80 mm).

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

Yabeiceras manasoaense Collignon, 1965

Figs 47, 51A–C

Yabeiceras manasoaense Collignon, 1965: 84, pl. 452 (fig. 1839). Matsumoto 1971: 144, pl. 24 (fig. 2), text-fig. 9. Klinger, Kennedy & Siesser, 1976: 162, figs 1–4.

Holotype

The original of Collignon (1965: 84, pl. 452 (fig. 1839)) from the zone of *Kossmaticeras theobaldi* and *Barroisiceras onilahyense* of Manasoa, Madagascar.

Material

BMNH C81465 and C81472, both from locality 145 in the Morrisvale area north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Dimensions

		D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
BMNH C81472	*c*	65,9(100)	35 (53,1)	19,7(29,9)	1,78	31,6(48,0)
	ic		31,8(48,3)	19,7(29,9)	1,61	
BMNH C81465	*c*	114,5(100)	42,0(36,7)	33,3(29,1)	1,26	54,0(47,2)
	ic		40,8(35,6)	33,3(29,1)	1,23	
	c	89,8(100)	39,3(43,8)	26,1(29,1)	1,50	41,6(46,3)
	ic		35,7(39,8)	26,1(29,1)	1,37	

Fig. 47. *Yabeiceras manasoaense* Collignon, 1965. BMNH C81465. ×1.

Description

The two specimens both retain recrystallized shell; the smaller shows details of early development previously unknown in the species. Coiling is evolute (the umbilicus comprises 48 % of the diameter) with the strong tubercles exposed within the umbilicus. The whorl section is depressed (breadth to height ratio is 1,61 intercostally, 1,78 at the tubercles), with the greatest breadth low on the flank between the ribs and at the strong tubercles, the cross-section reniform, with a broadly rounded venter and almost no flanks. The umbilicus is broad (48 % of the diameter), relatively deep, with a rounded wall.

There are seventeen massive conical to bullate umbilicolateral tubercles per whorl. At the smallest diameters visible these tubercles give rise to groups of two or three low, broad, straight prorsiradiate ribs that sweep forward across the ventrolateral shoulders and venter, terminating at the edge of the broad, shallow ventral grooves on either side of the low, broad, rounded siphonal ridge. The termination of the ribs is thickened but never develops into a tubercle; as size increases the ribs broaden and weaken, leaving the venter essentially smooth or with only faint undulations.

In the larger specimen the strong umbilical tubercles decline abruptly on the body chamber from a diameter of 95 mm onwards, beyond which ornament consists of distant, low, broad, concave flank ribs that decline and disappear over the venter. At the same time the whorl section becomes less depressed costally and intercostally, and the coiling becomes slightly eccentric.

The sutures are not exposed.

Discussion

The combination of massive, coronate, tuberculate inner whorls with a decline to a ribbed and smoothing adult whorl match well with the Madagascan holotype and the larger specimen from Japan described by Matsumoto (in Matsumoto & Inoma 1971: 144, pl. 24 (fig. 2), text-fig. 9). When compared with other species the massive tubercles of early-middle growth immediately distinguish this species from comparably sized *Yabeiceras magnumbilicatum*, *Y. costatum*, and *Y. ankinatsyense*. The tubercles of *Y. menabense* are spatulate rather than conical. In *Y. bituberculatum* the umbilicolateral tubercles are smaller, ribbing stronger, and ventrolateral tubercles better developed. *Y. transiens* sp. nov. has a polygonal whorl section, ribbing strongly developed, and umbilical, lateral, and ventrolateral tubercles. *Y. orientale* is less depressed and has relatively weaker tubercles and stronger ribs.

Occurrence

The types are from the Zone of *Kossmaticeras theobaldi* and *Barroisiceras onilahyense* of Manasoa (Betioky), Madagascar; the present specimens are from the St. Lucia Formation, Coniacian II, of Zululand, and it is also recorded from the Alphard Group off the southern Cape coast. It is also known from Japan, occurring in Teshio Province, Hokkaido.

Fig. 48. *Yabeiceras* aff. *manasoaense* Collignon, 1965. SAM–D1188B. ×1.

Yabeiceras aff. *manasoaense* Collignon, 1965

Figs 48–49

Compare

Yabeiceras manasoaense Collignon, 1965: 84, pl. 452 (fig. 1839).

Material

SAM–D1188B–C from locality 145 in the Morrisvale area north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Dimensions

		D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
SAM–D1188B	*c*	101,9(100)	37,8(37)	30,3(29,7)	1,25	49,8(48,9)
	ic		34,5(33,9)	30,3(29,7)	1,14	
		82,0(100)	32,5(39,6)	24,6(30)	1,32	37,8(46,1)
			29,0(35,4)	24.6(30)	1,18	
SAM–D1188C		97,4(100)	—(—)	27,5(28,2)	—	45,5(46,6)
	c	90,0(100)	35,6(39.6)	26.0(28,9)	1.37	41,0(45.6)
	ic		32,3(35,9)	26.0(28.9)	1.24	

Description

These two specimens are both wholly septate and retain recrystallized shell.

The coiling is very evolute, approximately 25 per cent of the previous whorl being covered. The umbilicus is broad (up to 49,8% of the diameter), shallow, with a low, rounded, outward sloping wall. The whorl section is depressed (costal breadth to height range 1,37–1,25; intercostal 1,24–1,14), with the greatest intercostal breadth low on the flank, the greatest costal breadth at the lateral tubercles.

Low, broad primary ribs, fifteen to sixteen per whorl at the smallest diameters visible (approximately 60 mm in SAM–D1188B and 50 mm in SAM– D1188C), arise at the umbilical seam and bear strong conical umbilicolateral tubercles housed in notches in the umbilical wall of the succeeding whorl. As size increases this tubercle migrates outward to a lower lateral position. The ventrolateral and ventral region is visible only from a diameter of 60 mm; in SAM–D1188C the tubercles are seen to give rise to single ribs or, more rarely, pairs of ribs, which terminate in a blunt, low, oblique ventrolateral clavus.

The outer whorl bears twenty primary ribs arising at the umbilical seam and bearing a strong conical lateral tubercle at the beginning of the whorl. This declines progressively, leaving only strong inner flank ribs in SAM–D1188B at a diameter of 100 mm, and a small, somewhat bullate midlateral tubercle in SAM–D1188C at the same diameter. In both specimens this tubercle gives rise to a broad, prorsiradiate concave rib that declines and effaces over the ventrolateral shoulder, leaving a smooth or gently undulose zone on either side

Fig. 49. *Yabeiceras* aff. *manasoaense* Collignon, 1965. SAM–D1188C. ×1.

of the strong, rounded siphonal keel and shallow flanking ridges, the outer sides of which are raised into weaker ridges.

The sutures are not exposed.

Discussion

Rounded rather than polygonal whorl section, absence of umbilical tubercles, loss of ventral tuberculation and entire, rather than nodate, siphonal keel readily distinguish this species from *Yabeiceras transiens* sp. nov., described above.

Y. crassiornatum sp. nov., described below, is more coarsely ribbed and tuberculate and retains its ribs and ventral tubercles to a much larger diameter. *Y. orientale* has rather similar inner whorls, as far as comparison is possible, but at a diameter of 80–90 mm loses all ornament and becomes compressed, whereas the present species retains its ornament. This loss of ornament and acquisition of smooth outer whorls at a relatively small size also allows our specimens to be distinguished from *Y. magnumbilicatum* (Basse), which also has rather fewer primary ribs per whorl in the early stages (thirteen in the specimen figured by Collignon 1965, pl. 451 (fig. 1835)).

Y. bituberculatum has altogether distinct, smooth adult whorls at a relatively small size, and utterly distinctive inner whorls. *Y. menabense* differs in its curious spatulate tubercles on the inner whorls and loss of ribbing at a size where these are retained by our specimens.

Y. ankinatsyense is more delicately ornamented with the ribs dominant over tubercles at the same size, as in *Y. costatum*.

The closest comparisons thus appear to be with *Y. manasoaense* Collignon; this, however, has much coarser lateral tubercles and a more depressed whorl section. In the holotype (Collignon 1965: 84, pl. 452 (fig. 1839)), coarse tubercles, fourteen to fifteen per whorl, persist to a diameter where the present specimens already show a decline and predominance of ribs or feebly tuberculate ribs that number 20 per whorl.

The larger specimen figured by Matsumoto (1971, pl. 24 (fig. 2)) has eighteen tubercles per whorl at a diameter of 100 mm and retains blunt ribs, thus more closely resembling our specimens. When compared with the two specimens from the same locality that have been referred to *Y. manasoaense* above, the coarser, more massive tubercles and whorls and distinctively different ontogenetic changes around the last whorl are again distinctive.

With so few specimens, we cannot tell if these differences are within the range of intraspecific variation of the species *Y. manasoaense* or whether a distinctive form is present. They are therefore referred to as *Yabeiceras* aff. *manasoaense*, acknowledging both the similarities to and differences from the Madagascan holotype and other material.

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

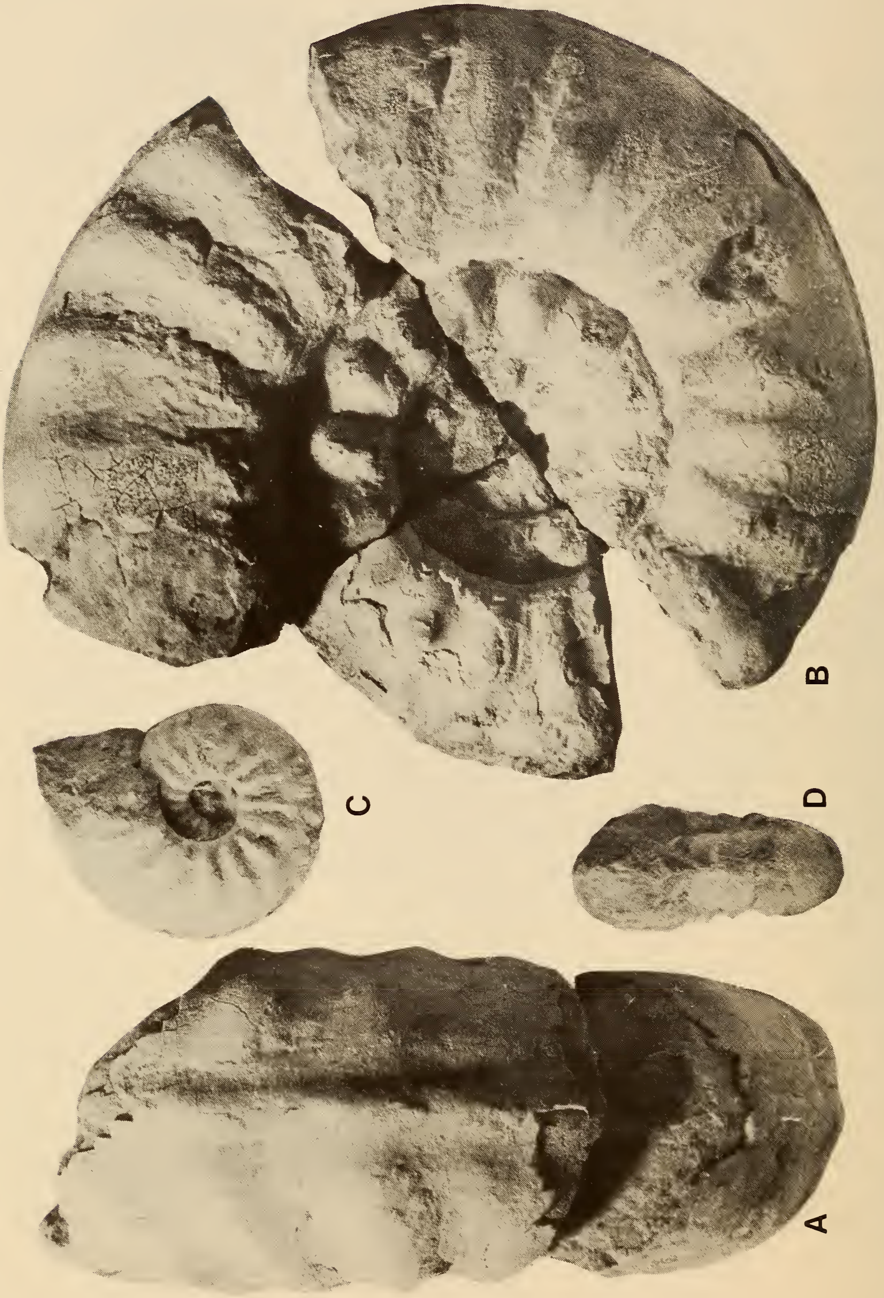

Fig. 50. A–B. *Yabeiceras crassiornatum* sp. nov. BMNH C81561. C–D. *Yabeiceras ankinatsyense* Collignon, 1965. SAS H196/3. All ×1.

Yabeiceras crassiornatum sp. nov.

Fig. 50A–B

Holotype

BMNH C81501, from locality 145 in the Morrisvale area, north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Etymology

Refers to the coarse ornament.

Dimensions

	D	*Wb*	*Wh*	*Wb* : *Wh*	*U*
c	137,00(100)	52,5(38,3)	44,0(32,1)	1,19	61,7(45,0)
ic		50,5(36,9)	44,0(32,1)	1,15	

Description

The coiling is very evolute, serpenticone, with a broad, rather shallow umbilicus that comprises 45 per cent of the diameter. The whorls are slightly depressed (whorl breadth to height ratio is 1,19 costally and 1,15 intercostally), the greatest breadth being well below midflank. The inner flanks are strongly rounded, the outer flanks flattened, converging to the broad venter. The inner whorls bear fifteen strong, broad, coarse primary ribs per whorl. These bear strong clavate tubercles that migrate progressively outward from an umbilicolateral to lower lateral position. At the smallest diameter visible, the beginning of the outer whorl, these tubercles give rise to broad, coarse, single ribs that terminate in blunt ventrolateral tubercles. There is a strong, broad, rounded siphonal keel flanked by broad, shallow grooves.

Traced around the outer whorl, the ribs remain coarse, distant and strong, totalling 18 or 19 per whorl. The lateral tubercles, initially strong, decline over the last third of a whorl and disappear, leaving only concave ribs on the flank. In contrast the ventral tubercles strengthen and persist as obliquely placed clavi on either side of the persistent coarse keel and shallow flanking grooves.

The sutures are not exposed.

Discussion

The persistence of coarse ribs and coarse ventral clavi to a very large diameter combined with the strong lateral tubercles in middle growth distinguishes this specimen from all other described forms; it is consequently afforded specific status.

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

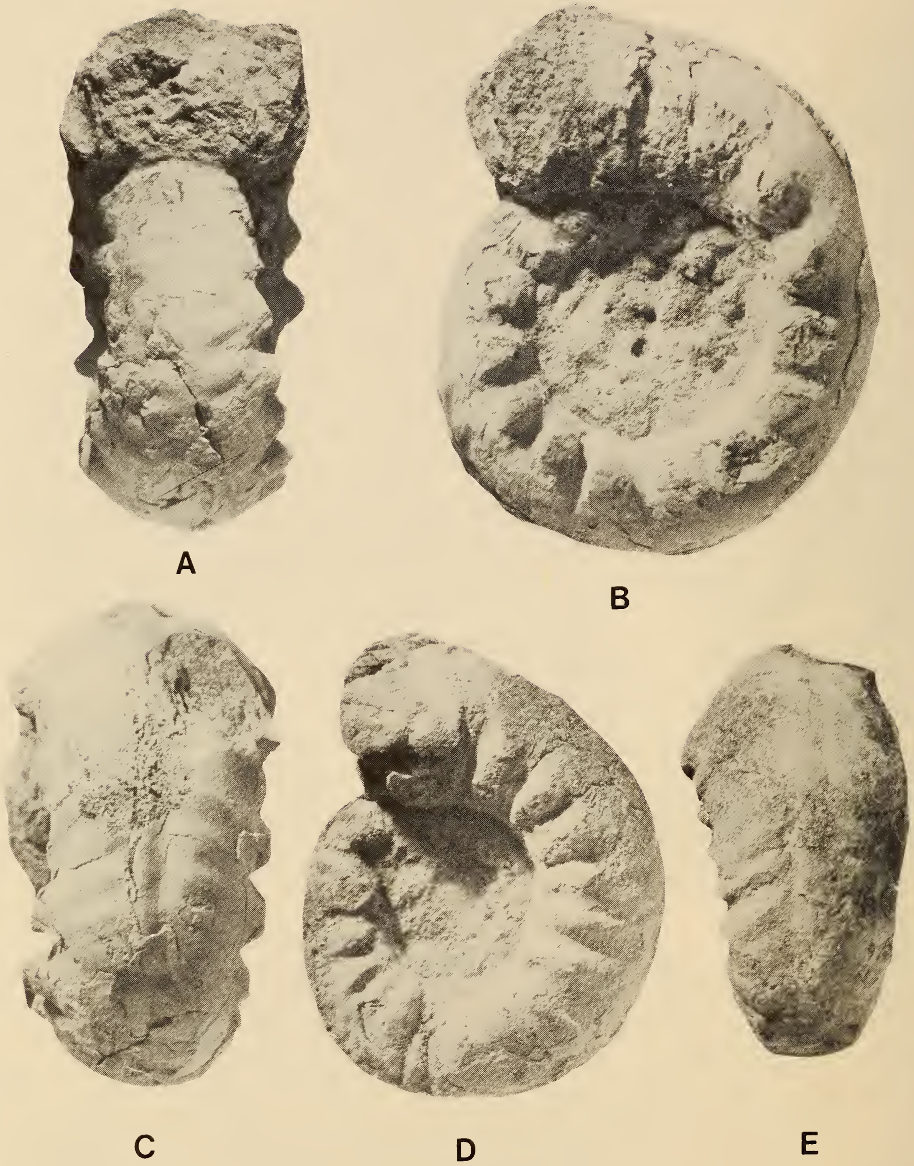

Fig. 51. A–C. *Yabeiceras manasoaense* Collignon, 1965. BMNH C81472. D–E. *Yabeiceras cobbani* sp. nov. BMNH C81542. All ×1.

Yabeiceras cobbani sp. nov.

Fig. 51D–E

Holotype

BMNH C81542, by monotypy, from locality 145 in the Morrisvale area north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Etymology

Named for Dr W. A. Cobban of the United States Geological Survey, Denver.

Material

Only the holotype.

Description

The single specimen is distorted, but retains recrystallized shell and has a maximum preserved diameter of 60 mm. The coiling is evolute, the umbilicus deep, and comprises an estimated 35–40 per cent of the diameter. The whorl section is depressed reniform in intercostal section with the greatest breadth low on the flanks. In costal section the greatest breadth is at the lateral tubercle; the estimated whorl breadth to height ratio is 1,7. There are an estimated eighteen primary ribs per whorl. These arise from umbilical tubercles of variable strength at the smallest diameter visible and migrate to a low lateral position around the outer whorl. They give rise to pairs of broad, coarse, concave prorsiradiate ribs that terminate in coarse, obliquely placed ventrolateral clavi. These are separated by a smooth, shallow groove from a broad, rounded siphonal keel that bears blunt clavi corresponding approximately to the ventral clavi. Interspaces between ribs are periodically deepened into constrictions, strong across the flanks but absent over the venter. There are four or five of these on the outer whorl.

Discussion

None of the described *Yabeiceras* species combines a coarse ornament of umbilicolateral, ventrolateral, and siphonal tubercles in the manner shown by this specimen and none develops constrictions.

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

Yabeiceras sp. indet.

Fig. 42F

Material

SAM–D1182, from locality 145 in the Morrisvale area north of Ngweni, Zululand, St. Lucia Formation, Coniacian II.

Description

This fragment shows an inner whorl with medium-sized conical lateral tubercles. The outer whorl has a whorl breadth to height ratio of 1,15 with rounded flanks and a broadly rounded venter. The flanks bear closely spaced concave flank ribs that die out across the ventrolateral shoulders. There is a strong, rounded ventral keel flanked by broad grooves, in turn flanked by slight lateral keels.

Discussion

The fragment has typically tuberculate inner whorls, as seen in many specimens of *Yabeiceras*, combined with a ribbed phase recalling *Y. costatum* at small diameters (e.g. Fig. 40A–C). It is, however, specifically indeterminate.

Occurrence

St. Lucia Formation, Coniacian II, of Zululand.

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